S101 Units 20 and 21

THE OPEN UNIVERSITY

Science: A Foundation Course

20 Diversity and Evolution
21 Communities of Organisms

The Open University

Science: A Foundation Course

Unit 20

Diversity and evolution

Prepared by the Science Foundation Course Team

The Open University Press

SCIENCE

S101 Course Team List

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1.1

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Table A List of terms and concepts used in Unit 20

Assumed from general knowledge	Introduced in a previous Unit	Unit No.	Introduced or developed in this Unit	Page No.	Developed in a later Unit	Unit No.
classification	adaptation	18	adaptive radiation	14	ecological niche	21
habitat	bacteria	18	adaptive resistance	22	myxomatosis	21
pelvis	chromosome	19	*Australopithecus*	32	uniformitarianism	26
	convergence	18	behavioural isolation	8		
	Drosophila	18, 19	canine teeth	31, 32		
	diversification	TV 18	cheek teeth	31, 32		
	evolution	18	class	11		
	gene	19	Cro-Magnon Man	37		
	genetics	19	endemic forms	19		
	mammal	18	evolutionary tree	10		
	morphology	18	family	11		
	mutant	18	fossil	22		
	mutation	18	genus (*pl.* genera)	11		
	natural selection	18	geographical isolation	7		
	population	18	Hominoidea (hominoids)	12		
	primate	18	Hominidae (hominids)	12		
	sulphonamides	16/17	*Homo erectus*	34		
			Homo habilis	34		
			Homo sapiens neanderthalensis	37		
			Homo sapiens sapiens	37		
			micro-evolution	22		
			macro-evolution	22		
			molar teeth	31, 32		
			mosaic evolution	35		
			order	11		
			palaeontology	22		
			phylum	11		
			Peking Man	35		
			premolar teeth	31, 32		
			race	6		
			Ramapithecus	31		
			reproductive isolation	6		
			speciation	6		
			species	11		
			subspecies	11		
			taxonomy	11		
			taxonomic hierarchy	11, 12		
			wild type	5		

Study Guide for Unit 20

This Unit varies quite considerably from one Section to another, both in the density of the factual information and in the nature of the concepts. The Sections on human evolution (Section 4.3 onwards) contain the greatest amount of factual information, and you will probably need to spend about a third of your study time for the Unit on them. If you are short of time, the Section on adaptive resistance, Section 4.1, is the least essential, and could be omitted. You are not advised to miss out Section 2, which deals with the taxonomic hierarchy, because the material covered in this Section will be referred to frequently in later Units.

The Home Experiment for this Unit involves the use of the moth trap, and should be performed some time after you have read Section 2.

In Section 4, you will need your *stereoscopic* viewer for looking at Filmstrips 20.2 to 20.5. Note that Frames 21 and 22 of Filmstrip 20.5 are for use with TV 20. Your ordinary viewer will be needed for Filmstrip 20.1, which comprises four Frames (1–4) referred to in the Unit text and three (5–7) for the *Home Experiment Notes*.

Introduction

The last two Units should have helped to give you an idea of the mechanism by which evolution comes about. In Unit 18 the theory of evolution by natural selection and the reasoning upon which it is based are described. Unit 19 deals with the mechanisms by which characters are inherited, and shows how a knowledge of these mechanisms is important for a proper understanding of natural selection. In this Unit we turn to a slightly different aspect of evolution—'evolution in action', that is, the course of evolution rather than the mechanism by which it occurs. (A rough analogy of these two different aspects of evolution can be found in a train drawing away from a platform. One might be interested in asking about the mechanism by which the train moves, that is, how the motor works; this is equivalent to looking at the mechanism by which evolution occurs, that is, natural selection. Alternatively, one might be interested in the movement of the train itself, that is, how its position changes with time; this would be equivalent to looking at the course of evolution.)

We shall start by asking the question, 'How do organisms become different from one another during evolution?' In answering this question we lead into a discussion of the process called 'speciation'. The fact that organisms do evolve into so many different forms means that biologists need a system for referring to and classifying different organisms. The discussion of speciation is therefore followed by a description of a system of classification. We then look more closely at the many different kinds of organism that are alive in the world today. Part of this subject is dealt with in the Home Experiment. The remainder is in Section 3, which discusses patterns of evolution, and in particular a phenomenon known as adaptive radiation.

Living organisms do not show directly the course that evolution has taken in the past. In the final part of the Unit consideration is given to how organisms have evolved over the ages. First of all we give a few examples of very rapid evolution in which organisms evolve over a matter of a few years. Then the evolution of one or two groups of organisms over millions of years is discussed in more detail. One of the most interesting examples to choose, from a purely human point of view, is our own evolution, and it is with the story of human evolution that the Unit closes.

1 Speciation

Study comment In this Section we ask why evolution results in organisms that diverge in their features as time passes. The events that lead up to diversification are described and the terms 'speciation' and 'species' are introduced.

The account of natural selection given in Unit 18 may have caused you to wonder why there are so many different kinds of organism alive in the world today. After all, if a mutation occurs that produces an organism whose phenotype is superior to the normal or *wild-type* organism, one would expect the mutant form to flourish and replace the normal form. Evolution, one would imagine, would proceed by one kind of organism replacing another. If that is so, then why is there not just one 'super-organism' in the world today, a magnificent mutant that has ousted all rivals? There are many reasons why this has not happened, and several of them are bound up with arguments from genetics that have to be left for other biology courses. However, there is one very basic and important reason, which needs to be discussed here. It is simply that the world is a changeable place and, as a result, populations of organisms often become isolated from one another.

wild type

Consider the following hypothetical example. Suppose that a population of organisms, perhaps of a particular kind of butterfly, live in a tropical forest, and that they are found in every part of that forest. Suppose that the conditions in the forest have been stable for millions of years so that the butterflies have become extremely well-adapted to life in that environment. This means that mutant forms that arise in the population are always or nearly always less fit than the existing butterflies, and so do not spread throughout the population. Under these conditions no new character will evolve.

Suppose, however, that over the course of a few thousand years the climate changes and becomes very much drier, so that the forest dies out and is replaced by scrub or desert, and that this happens everywhere except on two or three mountains, which remain sufficiently wet for the forest to survive. (This supposition is not fantasy; such events certainly did happen in parts of the world in the past.) What was once a big, well adapted, population of butterflies occupying a large, unbroken tract of forest would now be reduced to two or three small populations, confined to the forest regions on the mountain slopes. Where the forest had vanished in-between, the butterflies vanished too.

It would not be at all surprising if the conditions on two of these separate mountain tops were rather different: perhaps one mountain was further north and colder than the other; perhaps one was subject to different prevailing winds, and so on. Look at Figure 1. Suppose forest A was identical to the original unbroken forest, whereas B was colder, windier and wetter. The population of butterflies in B might not be very well adapted to that new climate and, assuming they did not become extinct, it would not be surprising if over many generations, natural selection favoured genetically new forms of butterfly. These would then spread throughout the population in forest B and so the butterflies in that forest would end up by being rather different from those in A. In place of the one kind of butterfly that existed before the change in climate, there would now be two.

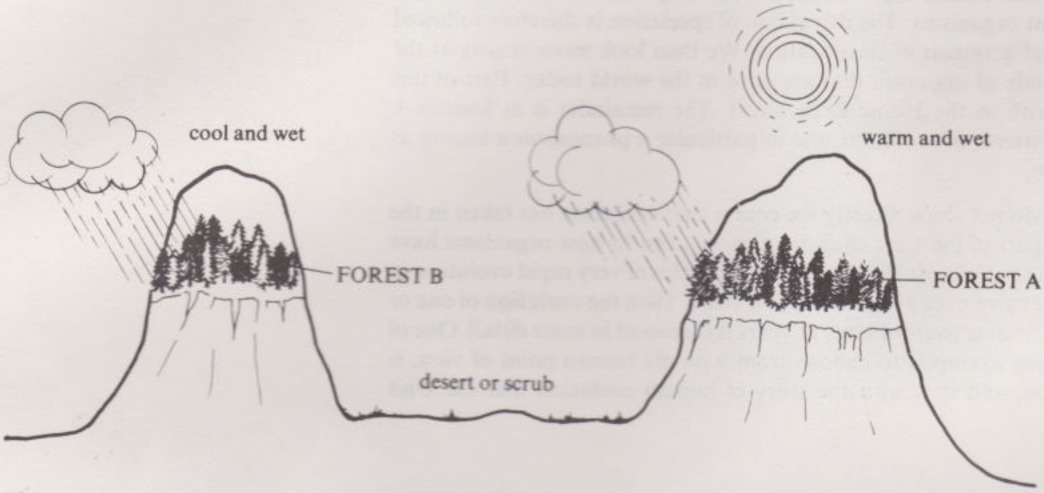


FIGURE 1 Different climates in two forest areas that were once part of a continuous tract of forest.

Suppose, now, that the climate changed yet again; perhaps it became wetter and warmer, and the forest grew again, joining together localities A and B. The butterflies in A and B move into the newly grown forest, and meet up again. What would happen? The answer would depend upon how different the two populations of butterflies had become during their period of isolation. If they had not diverged very much, then they would probably mate with each other, and a new, single, population of butterflies would be formed. Once again, there would be but one population of butterflies in the forest. If, however, the two populations of butterflies had diverged so much that they were not able to interbreed (remember, from Unit 18, that the definition of a population is a group of organisms of the same kind that live in one area and are capable of interbreeding), there would now be two genetically independent populations of butterflies within the same forest. Because the two populations of butterflies could not interbreed they could not exchange genes. They would be, to use the technical term, *reproductively isolated* from one another. Once the two populations were reproductively isolated they would evolve along their own separate ways; the characters of one population would not be mixed in with those of the other.

reproductive isolation

For a summary of the main points of this argument, refer now to Figure 2.

It should be clear that the crucial feature that allows two populations of organisms to evolve independently is that they should be reproductively isolated. When they are, they are said to belong to different *species*. The process by which species are formed, outlined above, is called *speciation*. When two populations of organisms are rather different in appearance but are not sufficiently distinct to be reproductively isolated they are said to belong to different *races*. (The American song sparrow provides a good illustration; see p. 8.)

speciation

race

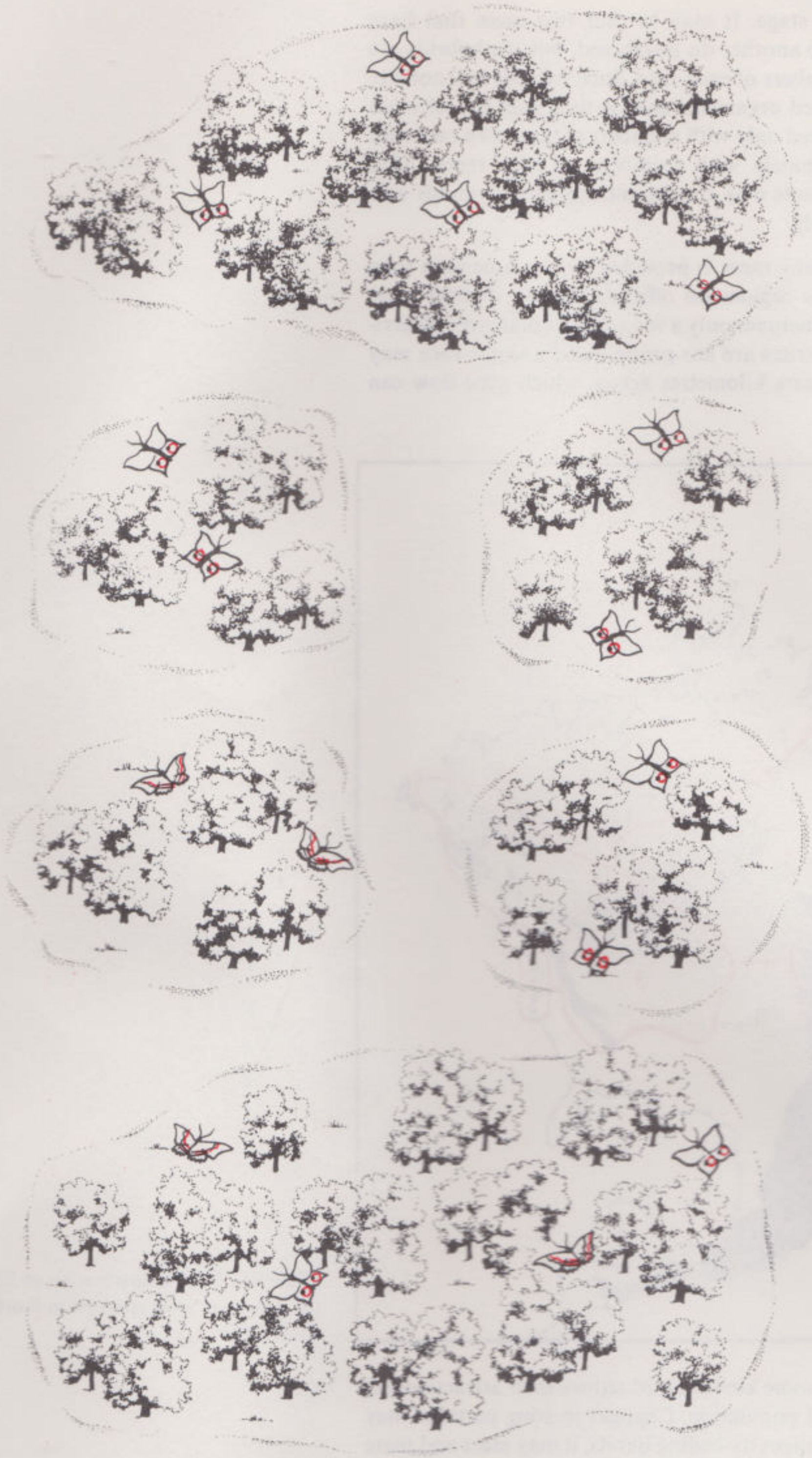


FIGURE 2 A possible explanation of how populations diversify as a result of geographical isolation.

1 Unbroken population of butterflies in forest.

2 Change in climate splits forest and butterfly population in two.

3 Differences in climate in the two areas result in the evolution of a different form.

4 Another change in climate causes the forest to join up again. If the butterflies are sufficiently distinct, they may not interbreed, so there are now two species. If they do interbreed there probably will be just the one species again.

geographical isolation

In the example of the forest-living butterflies, the cause of the initial *geographical isolation* of the two populations was a change in climate. Reproductive isolation can occur wherever a geographical barrier (e.g. mountains, deserts, water), or some other factor, brings about a discontinuity in the population.

If, for example, disease (or fire or a predator) effectively wipes out part of the population, dividing it into two, recolonization of the intermediate area may take time. During this period the 'outlying' population will exchange few genes with the rest. If conditions differ substantially in the areas occupied by the two groups the effects of selection on the relative frequencies of the genes in the groups may become apparent.

Such factors obviously encourage the formation of races from a single population. In areas where there are already distinct races the same factors will slow down the exchange of genes between the races. And once there are differences between races reproductive isolation may well arise, even if not immediately. When two races come together and fail to interbreed they are by definition reproductively isolated.

Sometimes there is an intermediate stage. It may be that two races that have recently come into contact with one another do interbreed, but the hybrids are much less fit than the pure-bred members of each race. Such hybrids will not fare well in comparison with the pure-bred organisms and, as time goes by, selection will favour those individuals who breed only with members of their own race over those who try to breed indiscriminately with members of both races. After sufficient time has elapsed, the two races may consist entirely of individuals who are completely isolated reproductively.

An example of a species that has many races is provided by the American song sparrow (Figure 3). In mountainous regions on offshore islands, distinct races have become isolated, each having sometimes only a few square kilometres of territory. In areas where geographical barriers are less pronounced a single race may have a territory of thousands of square kilometres across which gene flow can occur relatively unimpeded.

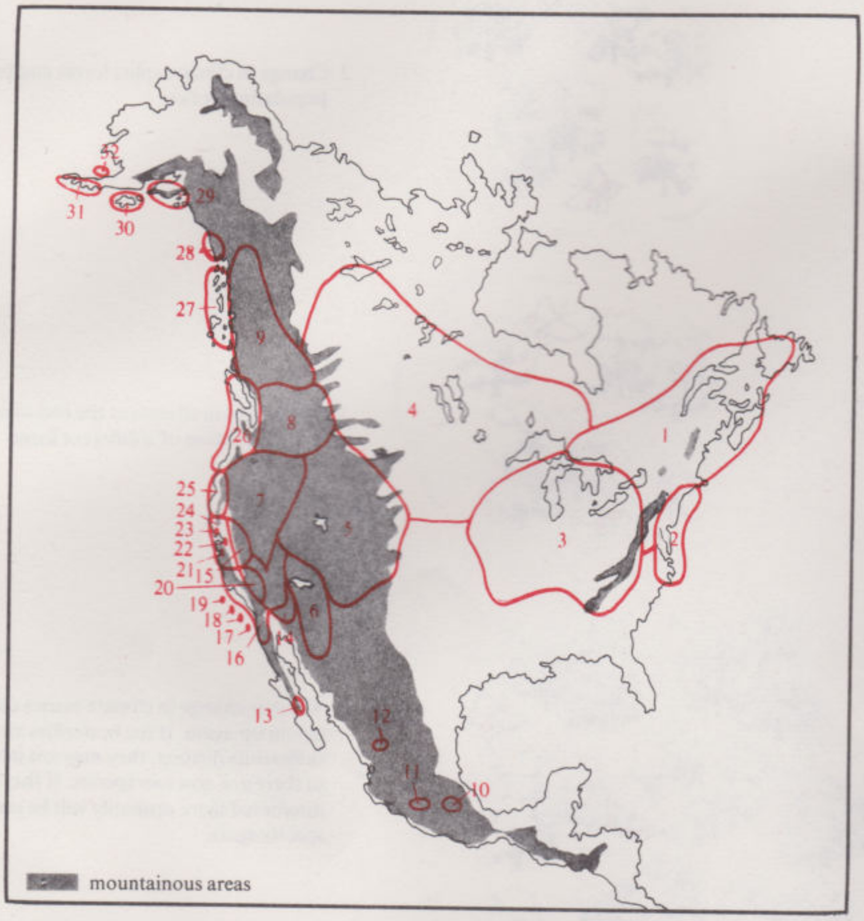


FIGURE 3 The distribution of 32 races of the American song sparrow in North America.

Small differences in the markings of some kinds of bird reduce their attractiveness as mates to members of the original population. Changes in song patterns may have the same effect. If an animal changes its feeding habits, it may meet and mate less frequently with members of the main population. Races of mosquitos apparently sharing the same environment may seldom or never meet if one group develops the habit of flying and feeding by day and the other carries out these activities in the evening or at night. Reproductive isolation may thus occur as a consequence of the animals' behaviour. Such isolation is known as *behavioural isolation.* Plants living in the same locality may be reproductively isolated if they flower at different times of the year. These, and many other small differences, may effectively isolate the members of one race (or part of a gene pool) from the rest. And selection will increase the divergence until they are no longer part of the same pool. But do they constitute a new species?

behavioural isolation

The test usually employed in deciding whether organisms that vary from one another are merely different races of the same species or constitute a different species is to see if they interbreed and produce fertile offspring *under natural conditions.* Once the genetic differences have become marked there may be no interbreeding, or else the offspring may fail to develop properly or may be infertile. Many instances of hybrid sterility are known. The mule (horse × donkey) is a

case in point. It must be bred from horses and donkeys each time, not from other mules. Reproductive isolation is complete; no genes will be exchanged between horses and donkeys. Sometimes, however, it is a question of degree. Domestic cattle can be crossed with American buffaloes, yaks and other relations. The hybrid bulls are sterile, but the cows are fertile when mated with domestic bulls, buffaloes or yaks. In two particular species of *Drosophila* there is merely a lowered fertility in the hybrids; but this, coupled with other isolating factors, means that under natural conditions the two species do not exchange genes. So, even failure to interbreed is not a simple and absolute criterion to use to distinguish separate species.

1.1 Objectives of Section 1

Now that you have completed this Section, you should be able to:

(a) Give the meaning of the terms 'species' and 'speciation'.

(b) Explain why reproductive isolation is necessary if populations of organisms are to diversify.

(c) Demonstrate an understanding of two mechanisms (geographical and behavioural isolation) by which reproductive isolation can be achieved.

To test your understanding of this Section, try the following SAQs.

SAQ 1 If two kinds of bird, one found only in South America and one found only in Australia, that are rather similar in appearance are caged together and found to breed, should they be classed as the same species? Give reasons for your answer.

Answers to SAQs begin on p. 42.

SAQ 2 Which one of the statements (i)–(vi) makes a correct assertion about speciation?

(i) Two races are said to have speciated if they interbreed when meeting after a period of geographical isolation.

(ii) Two races are said to have speciated if they interbreed without experiencing a period of geographical isolation.

(iii) Two races are said to have speciated if they fail to interbreed after a period of geographical isolation.

(iv) Two races are said to have speciated if they fail to breed because they are geographically isolated and so do not meet.

SAQ 3 Which of (i)–(iv) is the correct explanation of why reproductive isolation is necessary if populations of organisms are to diversify?

(i) Without reproductive isolation two races would evolve in the same direction.

(ii) Reproductive isolation prevents one race from competing with the other.

(iii) Reproductive isolation promotes the separate evolution of two races.

(iv) Reproductive isolation creates separate gene pools upon which selection can act.

SAQ 4 List three ways by which two closely related species of animals living in the same locality might be reproductively isolated by virtue of differences in their behaviour.

SAQ 5 List two common practices of modern industrial society in Britain that might bring about the geographical isolation of sections of a formerly continuous population.

2 The taxonomic hierarchy

Study comment In this Section we explain how evolution leads to some groups of organisms being closely related to one another and to others being distantly related. Biologists need to have a system of classifying organisms that reflects these differing relationships and allows easy reference to different organisms. The system used by biologists is described.

In Section 1 the method by which it is believed that species become distinct from one another was outlined. It needs little imagination to see that the process of divergence does not stop with the formation of species. With the passage of time, perhaps millions of years, species that are isolated from one another may become less and less similar. One would therefore expect to find among living organisms, which are, after all, the product of this evolutionary process, some species that are rather similar to each other and others that are very different from each other indeed. Refer now to Figure 4, which is an *evolutionary tree*, a semi-pictorial device that represents time vertically up the page and the evolutionary history of organisms as branches of a tree. Suppose that an ancestor of species A–F lived 100 million years ago (100 Ma), and that shortly after that time the ancestral population split into two distinct populations (at the point marked 1). One of these populations remained relatively unchanged to the present day, but the other split and diverged several times (at points 2–5) giving rise to species B–F.

evolutionary tree

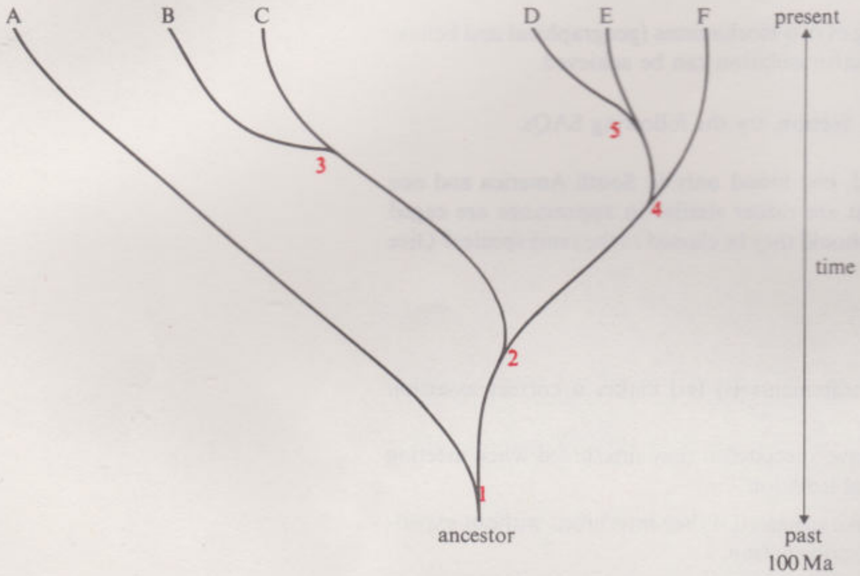


FIGURE 4 An evolutionary tree.

Species D and E diverged from each other only recently, and so are more similar to each other than either is to F. All three have more in common with each other than any of them has with B or C, and B and C have more in common with each other than either has with D, E or F. All five species have more in common with each other than any of them does with A.

Note, in Figure 4, that the closeness or distance of the relationship between two species is depicted on the evolutionary tree by the length of time that has elapsed since they diverged. The horizontal separation of the lines is not usually used to depict precise extents of relatedness, although, on the whole, species that are closely related to one another (such as D, E and F in Figure 4) are usually placed closer to each other horizontally than are more distantly related species (such as C and D). Note also that the trunk and branches of the evolutionary tree are drawn as single lines. This is the simplest way of drawing an evolutionary tree, but by no means the only way. Often broad bands are used instead of thin lines (see, for example, Figure 22). This latter method conveys better the notion that evolution proceeds by one *population* of organisms evolving into another, rather than one individual organism evolving into another.

Biologists need to have a way of referring to organisms that indicates how much those organisms have in common. Therefore, they have created a system that groups organisms together in a hierarchical manner. The major categories used in classifying organisms are listed on the opposite page.

Asterisks indicate the most important categories. (*Note* The terms can be spelt with either a capital or a lower-case letter; the practice varies from one authority to another.)

terms of the taxonomic hierarchy

phylum*
class*
subclass
superorder
order*
superfamily
family*
genus*
species*
subspecies

At the bottom of the hierarchy is *subspecies*, a term approximately equivalent to the term race, which you have already met. All organisms of the same species that live in a particular locality and are very similar to each other in morphology are put in the same subspecies. Different subspecies that nevertheless interbreed with each other, if and when they meet, are put in the same species. Groups of species that are very similar to each other in phenotype are put together in the next classificatory group, the *genus*. (The plural of this word, which is pronounced with a soft g, is *genera*.) Groups of similar genera are put together in the same *family*, and so the process goes on, with successively larger groups being created by the amalgamation of successively more diverse groups of organisms.

This system was first devised by the Scandinavian biologist Linnaeus (1707–1778), and since then the science of classifying organisms into groups, or *taxonomy*, as it is called, has developed into a substantial and intricate discipline within the field of biology. It is possible, in fact, to introduce still more ranks in the hierarchy than those listed, but there are more than enough for our present purposes. Figure 5 gives an example of how the classificatory system works in one group of animals,

taxonomy

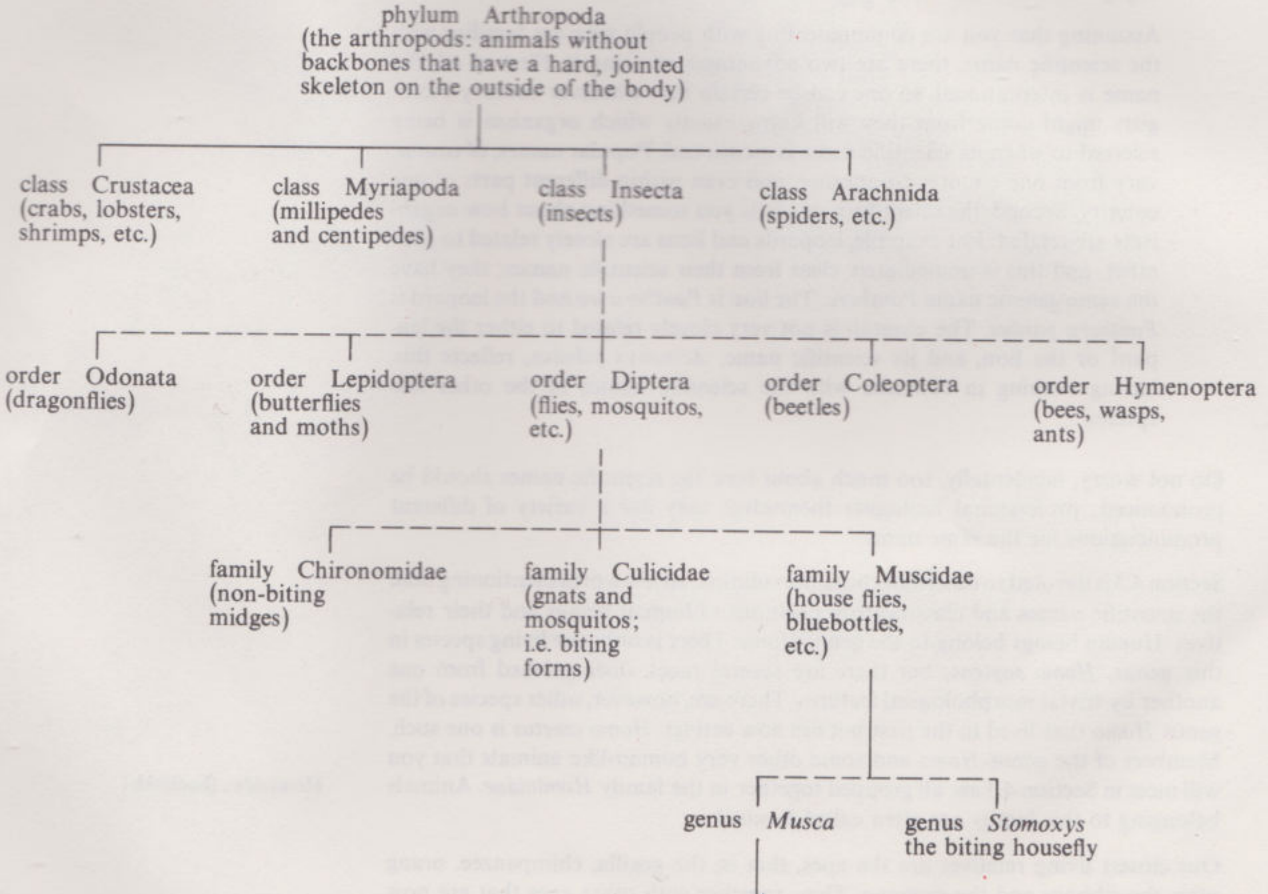


FIGURE 5 An example of the classification of a group of animals. (Do not try to remember any of the scientific names.)

the arthropods. These are animals that have the common feature of a hard, jointed skeleton on the outside of the body. (It is this skeleton that provides such an obstacle when we eat crabs and lobsters.) Do not try to remember any of the names in Figure 5. Simply note how the different categories fit together to form a *taxonomic hierarchy*. (The dashed lines indicate that the classificatory system has been simplified and that various groups have been left out.)

taxonomic hierarchy

Assessing how similar or dissimilar two organisms are, and whether they should be put into the same family or genus or not, is a highly subjective business, and one that is the source of endless debate among taxonomists. To a large extent, therefore, the levels of groups shown in Figure 5 are arbitrary. They are the consequence of trying to tidy into separate boxes the results of a continuous and gradual evolutionary process.

Along with this system of classification, Linnaeus devised a system for naming organisms. This system, somewhat expanded, is still used to this day; new organisms are named along Linnaean principles, following a set of internationally agreed procedures. Each species is given two Latin names. The first of these, the generic name, indicates the genus to which the organism belongs and the second, the specific name, indicates the species. It is conventional to write the names in italics, and to start the generic name with a capital letter and the specific name with a lower-case letter. When it is clear which genus is being referred to, it is often convenient to abbreviate the generic name to the initial letter followed by a full stop followed by the specific name. For example, *Drosophila melanogaster* might be abbreviated to *D. melanogaster*. Sometimes, it is also useful to denote different races of a species by adding a third name after the specific name (again in italics and beginning with a lower-case letter). For example, the English race of the wren is *Troglodytes troglodytes troglodytes*, whereas the St Kilda race of the wren is *Troglodytes troglodytes hirtensis*. (For other conventions, see Figure 5.)

> Can you think of two main advantages of using the scientific name of an organism rather than its popular name?
>
> Assuming that you are communicating with people who are familiar with the scientific name, there are two advantages in using it. First of all, the name is international, so one can be certain that whatever country biologists might come from they will know exactly which organism is being referred to when its scientific name is mentioned. Popular names, of course, vary from one country to another, and even within different parts of one country. Second, the scientific name tells you something about how organisms are related. For example, leopards and lions are closely related to each other, and this is immediately clear from their scientific names; they have the same generic name *Panthera*. The lion is *Panthera leo* and the leopard is *Panthera pardus*. The cheetah is not very closely related to either the leopard or the lion, and its scientific name, *Acinonyx jubatus*, reflects this, having nothing in common with the scientific names of the other two species.

Do not worry, incidentally, too much about how the scientific names should be pronounced; professional biologists themselves may use a variety of different pronunciations for the same name.

Section 4.3 is devoted to describing human evolution, so it is worth mentioning here the scientific names and classificatory positions of human beings and their relatives. Human beings belong to the genus *Homo*. There is only one living species in this genus, *Homo sapiens*; but there are several races, distinguished from one another by trivial morphological features. There are, however, other species of the genus *Homo* that lived in the past but are now extinct. *Homo erectus* is one such. Members of the genus *Homo* and some other very human-like animals that you will meet in Section 4.3 are all grouped together in the family *Hominidae*. Animals belonging to this family are often called *hominids*.

Hominidae (hominids)

Our closest living relatives are the apes, that is, the gorilla, chimpanzee, orang utan, the gibbons and the siamang. They, together with other apes that are now extinct, are put in a family of their own, the Pongidae (Figure 6). Both the Hominidae and the Pongidae have many more features in common with each other than they do with other animals, and so they are grouped together in a single superfamily, the *Hominoidea*. (Note that the ending is here -ea, not -ae). Members of the Hominoidea are often referred to as *hominoids*. (Again, note the important difference between hominid and hominoid.)

Hominoidea (hominoids)

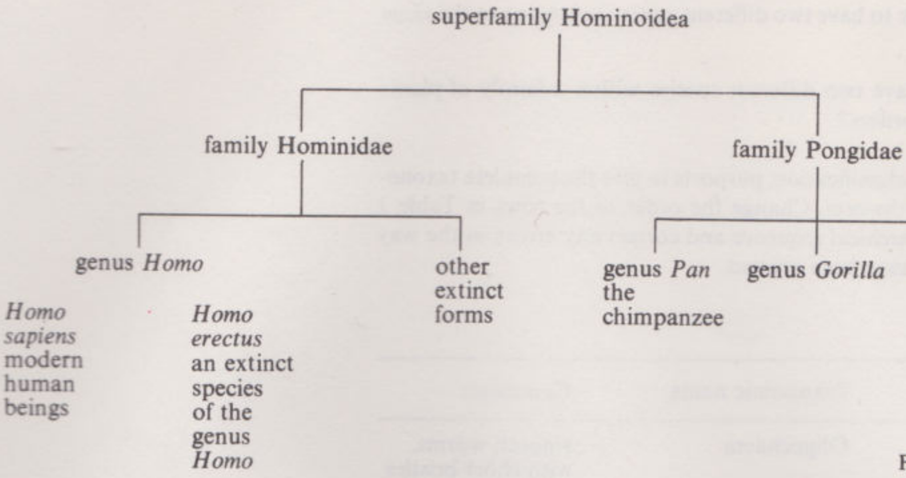


FIGURE 6 The classification of humans, apes and their relatives.

The Home Experiment for this Unit is concerned with the taxonomy of some common animals, and this is the most appropriate time to carry it out. It is not essential that you do the work now if it is inconvenient, as the remaining Sections of the Unit do not depend on material in the Home Experiment; but you should aim to complete the experiment before moving on to Unit 21.

2.1 Objectives of Section 2

Now that you have completed this Section, you should be able to:

(a) Draw and interpret an evolutionary tree.

(b) Understand the hierarchical principle of taxonomic classification.

(c) Remember the terms: phylum, class, order, family, genus and species; arrange these terms in their correct hierarchical sequence.

To test your understanding of this Section, try the following SAQs.

SAQ 6 In the evolutionary tree shown in Figure 7, A–F represent six different species. (The numbers are present simply for ease of reference.)

(a) Which two of the species are the most closely related?

(b) Are D and E more closely related than A and E? Give reasons for your answer.

(c) Are C and D more closely related than B and C? Again, give reasons.

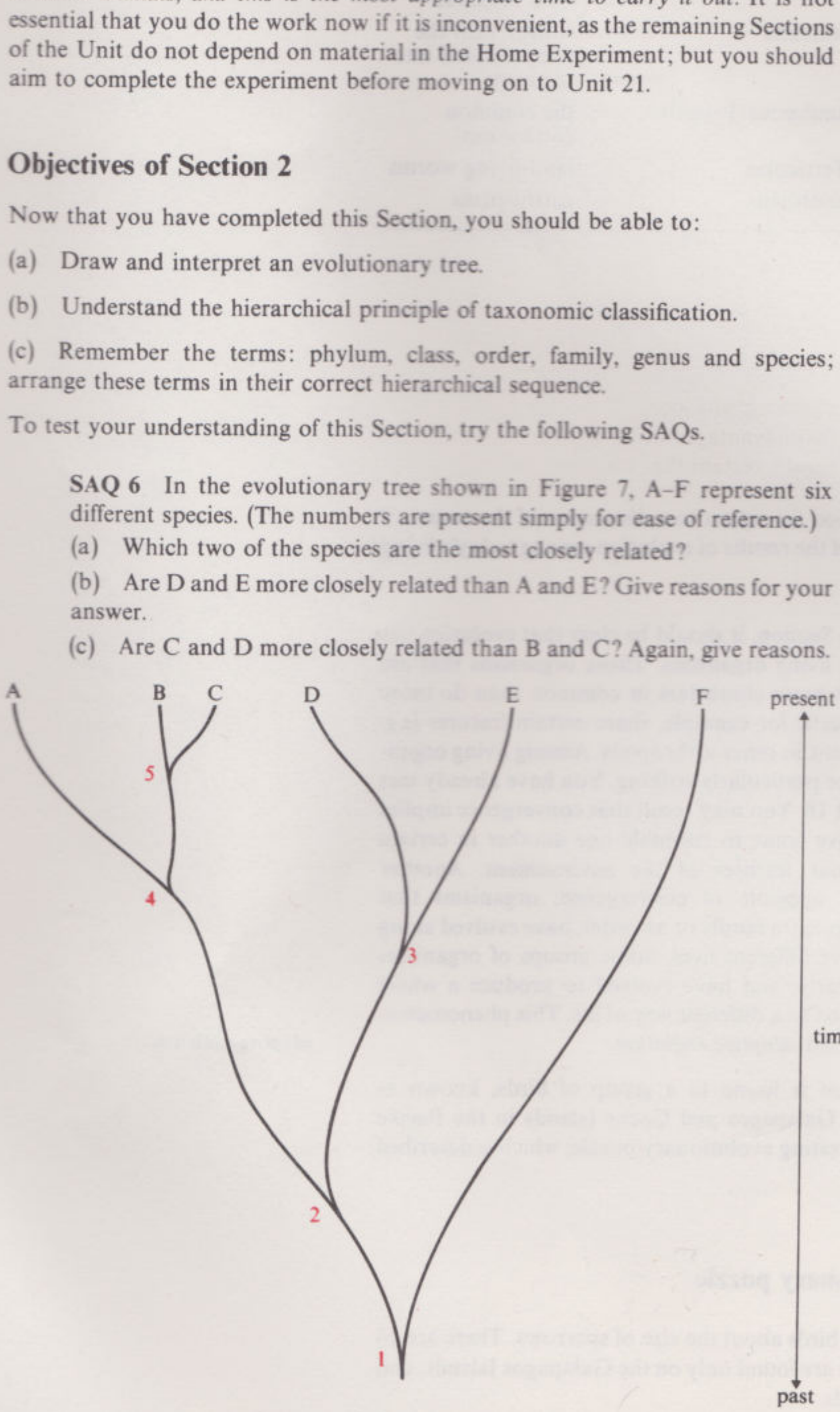


FIGURE 7 An evolutionary tree.

SAQ 7(a) Is it possible to have two different genera belonging to the same family?

(b) Is it possible to have two different species within a family of plants belonging to different orders?

SAQ 8 The following classification, purports to give the complete taxonomic position of the earthworm. Change the order of the rows in Table 1 to give the correct hierarchical sequence and correct any errors in the way the taxonomic names have been printed.

TABLE 1

Hierarchical sequence	Taxonomic name	Comments
class	Oligochaeta	smooth worms, with short bristles
family	Lumbricidae	the family of earthworms and their relatives
phylum	annelida	worms with the body divided into segments
species	lumbricus Terrestris	the common earthworm
order	Terricolae	land-living worms
genus	lumbricus	earthworms

3 Patterns of evolution

Study comment In this Section we return to a discussion of the course of evolution, and look at some of the results of evolution among today's living organisms.

From the discussion in the previous Section, it should be clear that evolution has resulted in certain patterns among living organisms. Those organisms that are closely related to one another have more characters in common than do more distantly related organisms. All insects, for example, share certain features (e.g. three pairs of legs) that are not present in other arthropods. Among living organisms there are other patterns that are particularly striking. You have already met one of them—convergence—in Unit 18. You may recall that convergence implies that distantly related organisms have come to resemble one another in certain aspects through adapting to similar features of the environment. Another pattern—divergence—is the exact opposite of convergence: organisms that belong to the same taxonomic group, say a family or an order, have evolved along different lines and have come to live different lives. Some groups of organisms show this divergence especially clearly, and have evolved to produce a whole range of different forms, each adapted to a different way of life. This phenomenon of conspicuous diversification is called *adaptive radiation*.

adaptive radiation

One example of adaptive radiation is found in a group of birds, known as Darwin's finches, that live on the Galapagos and Cocos Islands in the Pacific Ocean. These birds present an interesting evolutionary puzzle, which is described in Section 3.1.

3.1 Darwin's finches—an evolutionary puzzle

Darwin's finches are dully coloured birds about the size of sparrows. There are 14 species of these finches, of which 13 are found only on the Galapagos Islands, and one is confined to the Cocos Islands.

The Galapagos Islands lie 1 000 km west of the South American coast (Figure 8). They belong to Ecuador and, although they were given Spanish names in 1892, for continuity some biological writers still use the older English names given by seventeenth century buccaneers.

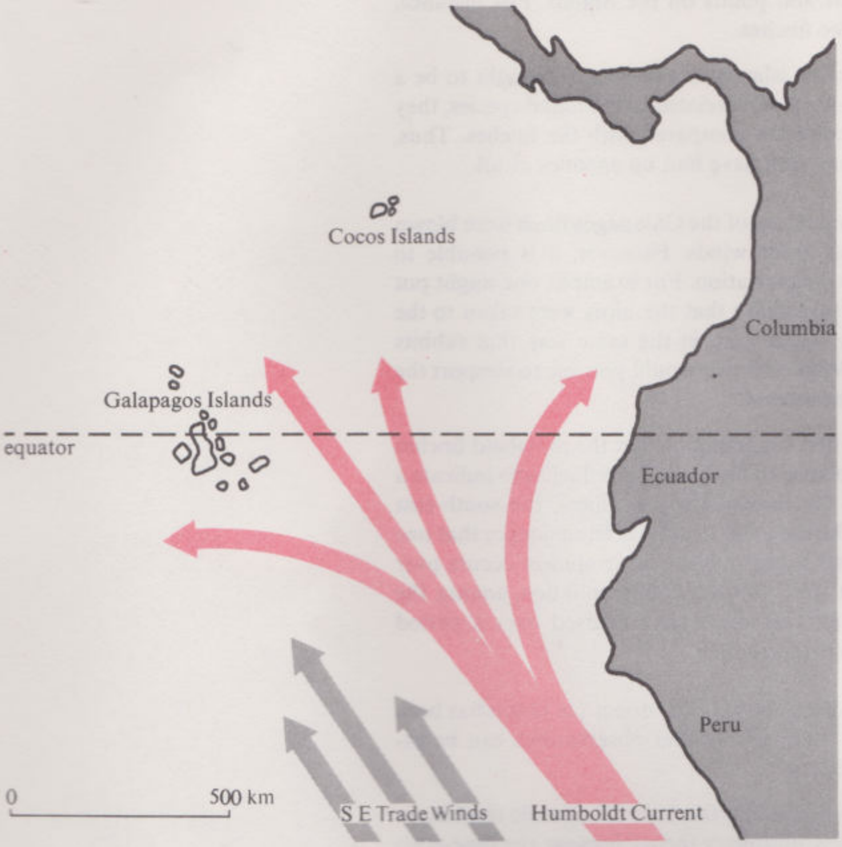


FIGURE 8 The Galapagos Islands.

The evolutionary puzzle is simply this—how does it come about that, although the finches resemble each other closely, different islands have different numbers of species of these finches and most islands have species of finches not found outside the Galapagos Islands? For instance, how is it that two of the three kinds of finch living on Hood Island are not found anywhere else, whereas all ten of the finches living on Indefatigable Island are found on at least one other island?

Evolutionary biologists more or less agree about the answers to this puzzle—their views are summarized in the Conclusions on p. 21. *If you are happy simply to accept these conclusions, turn straight to p. 21 and omit the passage between the single star(s) and the double stars.* However, the exercise on the next few pages gives you an opportunity to solve the puzzle of the Galapagos finches for yourself. The aim of the Exercise is to give you a better insight into science as a process rather than simply as a body of accepted 'facts'.

3.1.1 Exercise 1 Darwin's finches

1 How did the finches arrive on the Galapagos Islands?

★

The Galapagos Islands are volcanic in origin, so they were not inhabited by any living organisms when they emerged from the ocean many years ago. Among the plants and animals now living on them are species that do not occur anywhere else in the world. Thirteen of Darwin's finches are unique to these islands but nevertheless show sufficient resemblance to mainland finches to lead scientists to believe they had a common ancestor.

The various species of Galapagos finches differ in size and beak shape, but are very similar in most other respects—for instance, their plumage is similar in colour. They all build roofed nests and lay a similar-sized clutch of eggs. All are territorial and exhibit similar patterns of courtship and breeding behaviour. These facts indicate a close evolutionary relationship between the 13 species.

Figure 8 shows the direction of the currents and winds that affect the islands. It is thought that some of the original plant and animal 'colonists' arrived by water, drifting on floating tree trunks carried by the Humboldt current. Insects, small

seeds and birds could have been blown to the islands by the south-east trade winds. Finches do not normally fly long distances, so winds were probably needed to assist the finches' original ancestors in their passage to the islands. Such forms of travel are hazardous, to say the least, and this would account for the small numbers of different kinds of animals and plants on the islands. For instance, there are very few birds apart from the finches.

★

The main predators of the finches on the islands at present are thought to be a couple of species of owl. As these owls are closely related to mainland species, they are thought to be relatively recent colonists compared with the finches. Thus, before the owls' arrival the finches may well have had no enemies at all.

It has been suggested that the ancestors of the Galapagos finch were blown to the islands by the south-east trade winds. However, it is possible to suggest alternative methods of transportation. For example, one might put forward, in all seriousness, the possibility that the birds were taken to the islands by seventeenth century buccaneers, in the same way that rabbits were introduced to Australia. What evidence would you use to support the first suggestion and discount the second?

The evidence in support of the first suggestion is that the mainland finches show a sufficiently close resemblance to the Galapagos finches to indicate a common ancestry. Given that the finches are poor fliers, the south-east trade winds would have made the long flight feasible. The evidence that one might use to discount the second suggestion is that evolution occurs over very long periods of time and the amount of differentiation among the Galapagos finches indicates that they must have evolved over a period much longer than a few hundred years.

What sort of evidence has been used above? Is it 'direct', in that it has been based on experiments, or is it 'indirect', in that observations can be explained in terms of a general theory?

It is 'indirect' evidence. You will find that this sort of scientific thinking is used extensively in considering evolutionary theory because the time-scale of the evolutionary process is such that experiments cannot be set up to test hypotheses in the same way as in other areas of biology.

If arrivals from the mainland were frequent, would you expect the range of finch species on the islands to be similar to that on the mainland?

The Galapagos finches would show a range of species similar to that of the mainland. However, as Galapagos finches are found only on these islands, it can be concluded that there were very few episodes of colonization, maybe only one.

The colonizing flock could have included several different mainland species or just one species. If different species had arrived together, would they have changed markedly over the years? Do you think that colonization by a mixed flock is likely?

As they would not be competing for food, the different species would not have had to evolve very far from the original mainland species. They would therefore resemble the mainland finches more closely than they do; there would probably also be a greater variation among Galapagos species than is found. It is more likely that just one species arrived from the mainland.

What might be two reasons for the ancestors of the Galapagos finches establishing themselves on the island so successfully, in terms of the increase in their numbers and differentiation into so many different species?

The absence of predators and the absence of competition from other birds are reasons for success. In fact, the Galapagos Islands must have been an avian paradise with a wide range of food available and nothing to stop the finches making the most of it.

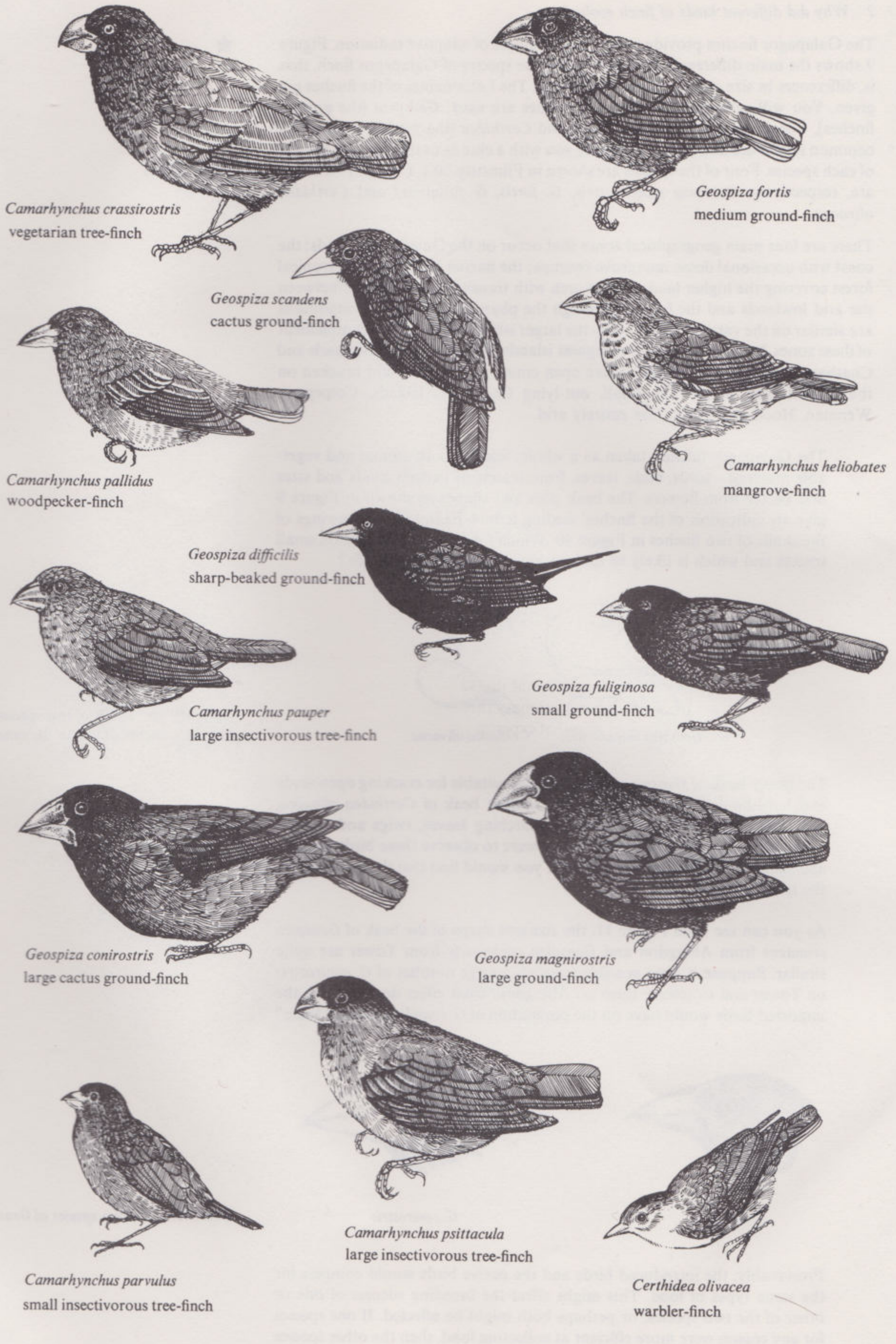


FIGURE 9 Species of Darwin's finches.

2 Why did different kinds of finch evolve?

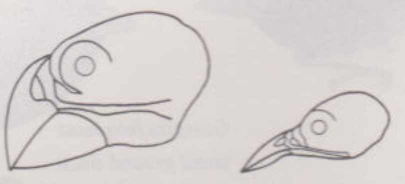
The Galapagos finches provide a very good example of adaptive radiation. Figure 9 shows the main differences that distinguish the species of Galapagos finch, that is, differences in size and the shape of the beak. The Latin names of the finches are given. You will note that three generic names are used: *Geospiza* (the ground finches), *Camarhynchus* (the tree finches) and *Certhidea* (the warbler finch). The common names are also given to provide you with a clue as to the diet and habitat of each species. Four of the species are shown in Filmstrip 20.1, Frames 1–4. These are, respectively, *Geospiza magnirostris, G. fortis, G. fuliginosa* and *Certhidea olivacea.*

★

Filmstrip 20.1

There are four main geographical zones that occur on the Galapagos Islands: the coast with occasional dense mangrove swamps; the barren lowlands; wet tropical forest covering the higher land; and an area with transitional vegetation between the arid lowlands and the forest. Although the physical and climatic conditions are similar on the various islands, only the larger islands have the full complement of these zones. In addition, the three highest islands, Indefatigable, Albermarle and Chatham, together with Charles, have open country with grass and bracken on the highest land of all. The small, out-lying Galapagos Islands, Culpepper, Wenman, Hood and Tower, are entirely arid.

The Galapagos finches, taken as a whole, feed on both animal and vegetable material—seeds, buds, leaves, fruit, insects of various kinds and sizes and nectar from flowers. The beak sizes and shapes as shown in Figure 9 give an indication of the finches' feeding habits. Examine the drawings of the skulls of two finches in Figure 10. Which finch is likely to feed on small insects and which is likely to feed on big insects and large seeds?



Geospiza magnirostris *Certhidea olivacea*

FIGURE 10 Skulls of two species of Darwin's finches drawn to the same scale.

The heavy beak of *Geospiza magnirostris* is suitable for cracking open seeds and hard-bodied insects, whereas the smaller beak of *Certhidea olivacea*, like that of warblers, is suitable for searching leaves, twigs and ground vegetation for small soft insects. If you were to observe these birds feeding, and examined their stomach contents, you would find that these are indeed the items on which they feed.

As you can see from Figure 11, the size and shape of the beak of *Geospiza scandens* from Abingdon and *Geospiza conirostris* from Tower are quite similar. Suppose it were possible to catch a large number of *G. conirostris* on Tower and to release them on Abingdon, what effect do you think the imported birds would have on the population of *G. scandens* already there?

G. scandens *G. conirostris*

FIGURE 11 Two species of *Geospiza.*

Presumably, the introduced birds and the native birds would compete for the same types of food. This might affect the breeding success of one or other of the two species, or perhaps both might be affected. If one species for any reason were more efficient at collecting food, then the other species would, over a period of generations, die out. If both species were equally efficient, then it might be that both species would continue to live and breed on the island, but in reduced numbers.

Table 2 shows the islands ranked in order of size, with the smallest at the top. It also shows the area of each island and the number of different species of flowering plants that are native to each island (i.e. ignoring those species that have recently been introduced by human beings). The total numbers of breeding species of finches found on each island are listed in the fourth column. Can you suggest an explanation for the difference between Tower (4 species) and Indefatigable (10 species)?

TABLE 2 The areas and numbers of species of native flowering plants and of finches on each island of the Galapagos

Name of island	Area (km^2)	No. of native flowering plants	No. of species of finches seen to breed on the islands
Culpepper	2	11	3
Wenman	3	20	5
Jervis	5	81	9
Tower	17	40	4
Duncan	18	89	9
Barrington	24	60	8
Hood	58	96	3
Abingdon	60	85	9
Bindloe	130	45	8
Charles	171	227	11
Chatham	552	221	8
James	572	185	10
Narborough	635	90	10
Indefatigable	905	306	10
Albermarle	4 607	244	11

Tower is small; it has only one zone, an entirely arid one, and has relatively few native species of flowering plants. Indefatigable is larger and contains highland—that is, it has a greater number of zones—and it has many more native species of flowering plants. It can thus provide habitats for a greater number of species, and a greater diversity of food plants.

Hood seems to have noticeably fewer species of finch than islands of similar size (i.e. those ranged near it in the Table). Can you suggest a reason for this? Consult Figure 12 (overleaf).

Hood lies to the south-east of the main group of islands. The birds, which do not normally fly far anyway, would have the extra difficulty of flying against the prevailing trade wind. Also, Hood has fewer zones than other islands of comparable size and so would provide a smaller range of habitats for the finches.

3 Why are there different finches on different islands?

There is a striking amount of variation within each species. For example, individuals of the ground finch *Geospiza fortis* are so variable in their beaks that they were, for a long time, considered to belong to at least two or possibly three separate species. However, it was eventually established that they belonged to the same species because they are still able to interbreed. The classification of the finches at the subspecies level is somewhat arbitrary, but it is possible to distinguish a number of different 'forms' in about half the species. Many of these forms are found only on one (or occasionally two) islands that are close to one another. The term used to describe them is *endemic forms.*

endemic forms

Figure 12 shows the number of endemic finch forms over the total number of resident forms on each island or pair of islands. Notice that the percentage of endemic forms ranges from 67 down to zero.

Consider the islands where a quarter or more of the finches are endemic. Are there any features that these islands have in common that might explain the high values? (In addition to considering the evidence for this question, you will also find it helpful to refer to the description of the islands given in question 2 and to look at Figure 12.)

The islands concerned are: Culpepper and Wenman, Abingdon and Bindloe, Charles, Chatham, Tower and Hood. All (except Chatham) are small islands and all are more or less isolated from their neighbours. In addition, the range of habitats is small—several of these islands are uniformly arid.

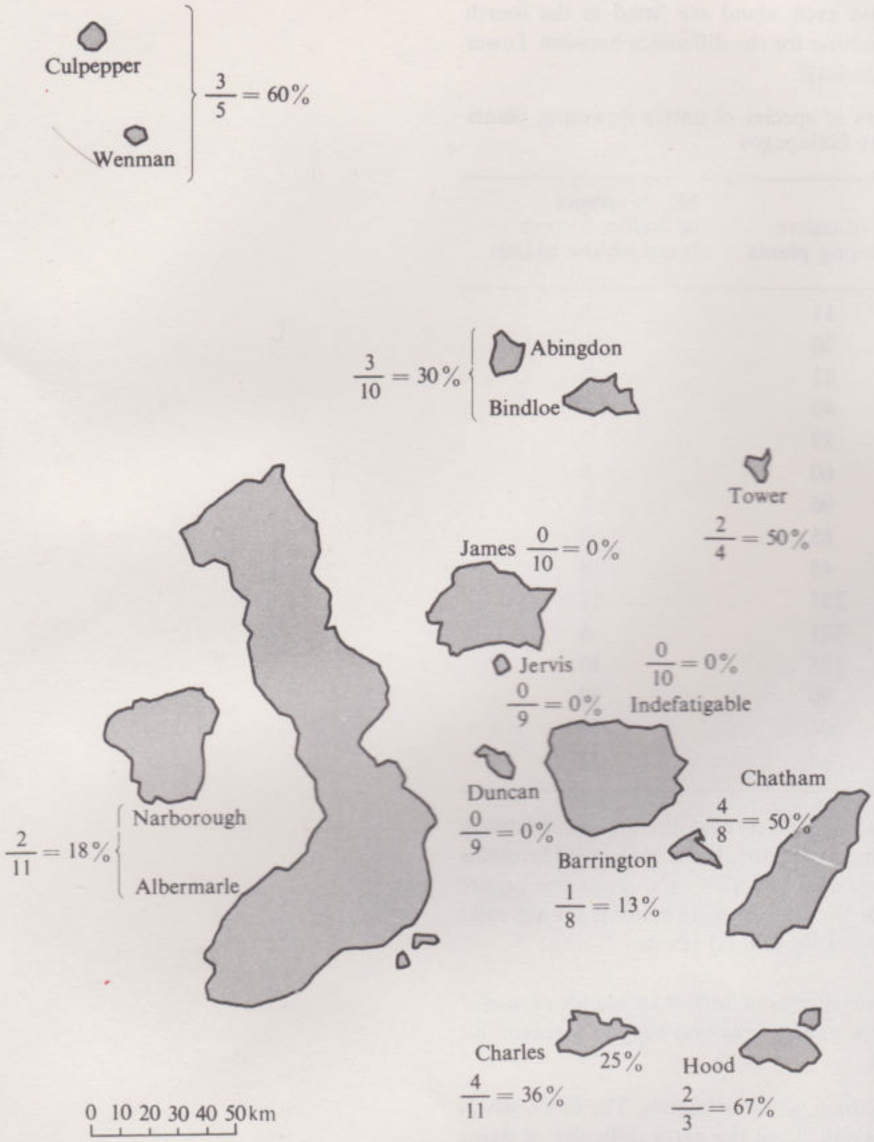


FIGURE 12 The percentage of endemic forms of Darwin's finches on each island. (Each fraction gives the number of endemic forms over the total for that island.)

Consider in turn (i) the small size of the islands and the uniformity of environmental conditions (ii) the isolation of the islands.

Try to decide how, if at all, each might explain the high proportion of endemic species on these islands.

(i) does not explain the high percentages of endemic forms, although the uniformity of environmental conditions might lead to the development of a small number of species on each island, as discussed in question 2.

(ii) The isolation of the islands could lead to the development of a high percentage of endemic forms. An argument supporting this conclusion would be that the islands are isolated and their nearest neighbours are 50–60 km away; finches are weak flyers, and so colonization of these isolated islands would be rare (equally, movement off the islands would be rare). Hence, once they had colonized an island, the forms would be likely to develop in ways not found on other islands—so the population would contain a high percentage of endemic forms.

Does this explanation fit in with the proportion of endemic forms on Albemarle and Narborough, James, Barrington and Indefatigable? How do you explain the very low percentage of endemic forms on Jervis and Duncan (see Figure 12)? ★

The explanation fits the pattern of low percentages of endemic forms in the south-western group of islands. The islands are close together, so birds could easily fly from one to another. One might expect a small number of species on Jervis and Duncan as they are small islands with a uniform environment; but there will not be any endemic forms because these islands are too close to other islands. ★★

Conclusions

Answers to the questions we have asked, and other similar questions, make it possible to put forward an explanation of the distribution of Darwin's finches and of the differences between them.

Initially, the islands were colonized by finches from mainland South America—possibly blown, or at least assisted by wind. In view of the isolation of the islands, colonization probably happened only a few times, perhaps once only.

As the islands were uninhabited, and there were probably no other small birds on them, the colonizing population was able to feed and reproduce, and the finch population expanded. Owing to the wide range of food available, it also diversified, different sections of the finch population becoming adapted to feeding on different types of food.

Distant islands were possibly colonized by finches from the main group of islands, which, being closer together, shared the same finch fauna. Probably, not all varieties of finch arrived on the distant islands; or, if they did arrive, some may have found the islands already occupied—they would have had to compete for food and other resources with the resident finch populations. So the more distant islands have a higher percentage of endemic forms of finch than the islands closer together in the central group.

Of course, this explanation of the present state of affairs, although fitting the observations, contains a number of assumptions and speculations. It is not possible to know for certain the course of evolution of Darwin's finches, and all that can be done is to put forward a more or less plausible guess.

Charles Darwin himself wrote (in *The Voyage of the Beagle*):

> I never dreamed that islands about fifty or sixty miles apart, and most of them in sight of each other, formed of precisely the same rocks, placed under a quite similar climate, rising to nearly equal height, would have been differently tenanted. It is the circumstance, that several of the islands possess their own species of the tortoise, mocking-thrush, finches and numerous plants, these species having the same general habits, occupying analogous situations, and obviously filling the same place in the natural economy of the archipelago, that strikes me with wonder.

3.2 Objectives of Section 3

Now that you have completed this Section, you should be able to:

(a) Give the meaning of the term 'adaptive radiation', and recognize examples.

(b) Understand the importance of geographic isolation for speciation.

To test your understanding of this Section, try the following SAQ.

SAQ 9 Recall from Unit 18 that the peppered moth *Biston betularia* exists in different colour forms, and that different colour forms have been shown to be adaptations to different types of habitat. Is this an example of adaptive radiation?

4 The history of evolutionary change

Study comment In this Section we trace how organisms have changed their morphology with the passage of time. We deal with two rather different situations: the first consists of rapid, small-scale, evolutionary changes over the course of a few generations; the second consists of much larger-scale evolutionary changes that have occurred over millions of years.

All of the discussion about evolution so far in this Unit has concentrated upon organisms that are alive at present rather than organisms that were alive in the past. By studying the diversity of living organisms it has been possible to make guesses about the evolutionary events that occurred among the ancestors of living organisms. The trouble with this sort of approach, however, is that it can provide only indirect evidence about the course that evolution took. In order to get rather more direct evidence one really needs to look at the changes that occur in organisms over a period of time. There are two ways of doing this. One can look at a population of organisms over as many generations as possible to see whether the characters of the organisms change. As humans have been looking for such changes only since Darwinian times, the time available to detect evolutionary changes in organisms by this method is rather small; this means that it is possible to pick up only fairly small-scale evolutionary changes. These small-scale changes are sometimes called *micro-evolution*. An alternative method is to look at the remains of organisms that are preserved in the rocks of the Earth. These remains are called *fossils*, and they may be preserved, if the conditions are appropriate, for hundreds of millions of years. (The study of fossils is called *palaeontology*, and those who study fossils are called palaeontologists. How old the remains of an organism have to be to qualify as a fossil is a matter over which people disagree. In this Unit, remains that are over 10 000 years old will be regarded as fossils. The word fossil is often used to refer not only to the remains of an organism, but also to other traces of life that have been preserved, such as an animal's footprints and the tools manufactured by early human beings.)

micro-evolution

fossil

palaeontology

Over such a length of time, it is possible to detect very large changes in the morphology of organisms, and for this reason such evolution is sometimes referred to as *macro-evolution*. The disadvantage of working with fossils is that usually only the hard parts of the organism are preserved—the bones and teeth of mammals, for example, and the seeds and pollen grains of plants.

macro-evolution

Fossils give a very incomplete picture of evolution for another reason. Only a minute fraction of all organisms that ever lived have been preserved as fossils, simply because the special conditions that are needed for such preservation occur rarely. This means that in only a few instances has it been possible to find a complete sequence of fossils that shows how the morphology of a group of organisms has changed gradually over long periods of time. More usually, the fossil record, as it is called, is rather or very incomplete, so that it is not at all easy to trace all the changes that have occurred in the evolution of a particular group of organisms.

Both micro-evolutionary and macro-evolutionary studies have drawbacks, therefore, as well as advantages, and it is important to use both types of study to supply evidence about the course of evolution. The next two Sections give examples of such evidence obtained from micro-evolutionary and macro-evolutionary studies, respectively.

4.1 Adaptive resistance

Some of the most striking examples of micro-evolution occur when a population of organisms is exposed for the first time to a harmful agent, such as a disease-causing organism or a toxic substance. At first, few of the organisms in the population are able to survive the activity of the harmful agent, but after a few generations these organisms multiply so that the population builds up again and consists almost entirely of organisms that are resistant to the harmful reagent. Such a phenomenon is called *adaptive resistance*. For example, *Staphylococcus aureus* is a common bacterium found on human skin, in putrefying matter and elsewhere. If it gets into human tissues it is pathogenic, that is, it may multiply

adaptive resistance

faster than the body's defences can destroy it, attacking the tissues and producing poisonous waste products. Depending on where it happens to be, it may be the causative organism of a sore throat, boils or fatal blood poisoning.

This bacterium, in common with other staphylococci, is generally very sensitive to the antibiotic* penicillin, even in quite small doses. However, when a dose of penicillin just large enough to 'cure' the disease is used, some individuals will become resistant as a result of a mutation and a number of these are likely to survive. They will not necessarily succeed in multiplying into large numbers (causing a relapse in the patient); the normal bodily defence mechanisms may keep them in check. Nevertheless, they will be there in small numbers, perhaps in the discharge of a healing boil or the saliva of a recent victim of a septic throat. Eventually, one such resistant bacterium may infect another victim, and it will be found that the disease does not respond to treatment with the normal dose of penicillin. Usually a very much larger dose will work, and so will be used. Resistance to very large doses requires a further mutation. But once again, as long as the concentration of the antibiotic is too low to be lethal to all the bacteria, the selection process will continue. This time selection will favour bacteria resistant to very large doses, often as large as it is safe to prescribe. This is why, incidentally, it is essential to 'finish the bottle' of prescribed antibiotic; if you do not, circumstances are being created that are ideal for the evolution of antibiotic-resistant strains of bacteria.

It is in this way that modern medicine produced the 'hospital staph', a very tough organism, with the result that the level of post-operative infection—which had fallen very low indeed in the early days of antibiotics—has risen considerably. The first signs of staphylococcal resistance appeared soon after penicillin became extensively used in hospitals, as Table 3 shows.

TABLE 3 The incidence of penicillin-resistant infection at a general hospital

Date	No. of patients with staphylococcal infections	No. of patients with penicillin-resistant strains
Apr.–Nov., 1946	99	14
Feb.–June, 1947	100	38
Feb.–June, 1948	100	59

By 1950, a majority of staphylococcal infections in all British general hospitals were resistant to penicillin. Subsequently, in certain staphylococci, resistance to all the major antibiotics has appeared, often as a triple resistance; that is, the same strain is resistant to penicillin, tetracycline and streptomycin. Fortunately, not all the strains of *S. auraeus* have produced such a dangerous triple resistance.

It is interesting to note that the much more dangerous bacterium *Streptococcus*, which was producing strains resistant to treatment with sulphonamides (Units 16 and 17, Section 5.1) has fortunately so far failed to produce a penicillin-resistant strain. There are, however, mutant strains resistant to tetracycline. Similarly, the bacterium causing the venereal disease gonorrhoea produced, as a result of selection, strains resistant to sulphonamides; more recently, strains with partial resistance to penicillin and streptomycin have emerged. Figure 13 (overleaf) shows the dramatic rise in infections by resistant strains of *Salmonella typhimurium*, the causative organism of food poisoning.

One can see, with the benefit of hindsight, that the incidence of this resistance might have been much reduced if antibiotics had not been prescribed unless really necessary and, more important, if larger doses had been used in the first place so that there was little chance of survivors.

In modern medicine, therefore, it has to be accepted that any pathogenic bacterium may give rise to strains resistant to almost any antibiotic. This means that the situation is always dynamic: new strains evolve; new antibiotics are produced to

* Antibiotics are a group of substances, produced mainly by moulds, that prevent bacteria from growing. They include penicillin, streptomycin and a group of antibiotics called the tetracyclines.

beat them. Slight changes in the structure of the drug are sometimes sufficient to make it effective against a new strain, and by an empirical process of 'molecular roulette' and by testing, research departments in the pharmaceutical industry and elsewhere have been able to keep ahead of the adaptive changes in the bacteria.

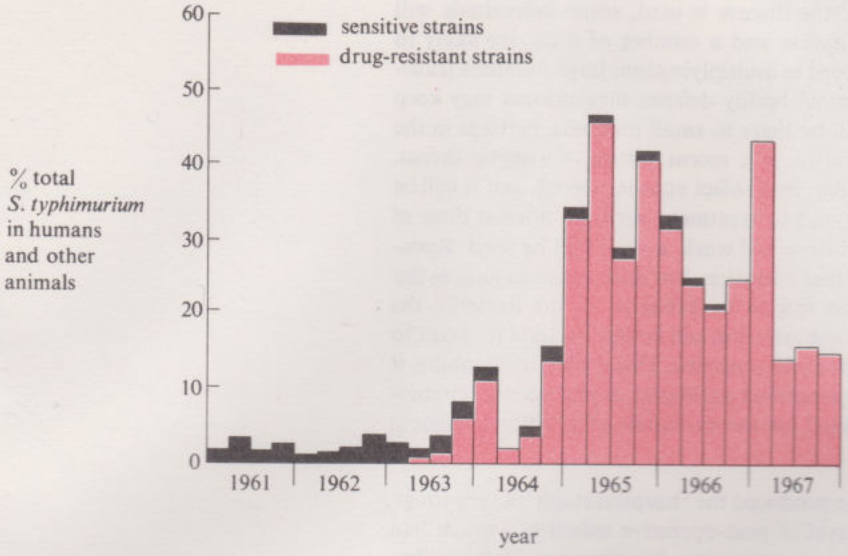


FIGURE 13 The incidence of drug-resistant strains of the *S. typhimurium* type 29 bacterium, which causes food poisoning in humans and other animals. (The incidence is expressed as a percentage of the total number of infections that are diagnosed.)

Resistance to DDT

A similar selective process has occurred among several insect species. As early as 1947, reports began to appear of strains of housefly that were resistant to the chemical DDT. (The chemical name for this substance at the time of its discovery was dichlorodiphenyltrichlorethane, for which DDT was an abbreviation. Its correct, modern chemical name is 1,1,1-trichloro-2,2-bis-(4-chlorophenyl)ethane; see Units 16 and 17, Section 5.2.) This chemical in very low concentrations is poisonous to most insects, and its introduction as an insecticide two or three years earlier had marked a real breakthrough in pest control. However, in countries all over the world, populations of flies soon appeared that were not killed by DDT in the concentrations originally used. As with the bacterial example just discussed, to be effective the dose had to be raised; but this was only possible within limits, as very large doses of DDT are not safe for either humans or domestic animals (indeed, at the present time, DDT is considered undesirable even in quite small doses). As a result, other chemicals have had to be developed to replace DDT in many parts of the world.

Under laboratory conditions, a significant degree of resistance has been evolved within three generations in the housefly by a process similar in principle to that used to produce antibiotic-resistant bacteria.

DDT-resistant strains have also appeared in many other insects, including some mosquitos, body lice, bedbugs and cockroaches. Some insects have even evolved strains resistant to poisons such as prussic acid and lead arsenate.

Resistance in mammals

It is not only such prolific organisms as bacteria and insects that are able to adapt fast enough to embarrass people in their attempts to exterminate them. Recently mammalian pests have provided similar examples.

For some years the brown rat (*Rattus norvegicus*) has been very effectively controlled by a poison known as Warfarin. However, in recent years strains resistant to Warfarin have appeared. The spread of this resistance through the brown rat population in Britain is described in TV 19.

A second example is provided by the rabbit. This animal has been something of a pest of arable crops and grassland in Europe for 200 years, though offsetting its nuisance value somewhat by providing a source of food and fur. It became a far more serious pest after its introduction to Australia, where the tremendous efficiency of its reproductive system compared with that of the native mammals enabled it to multiply almost unchecked.

Attempts were made both in Australia and Europe to control rabbits by the introduction of a virulent virus disease, myxomatosis, which had up till then been confined to another species of rabbit in South America. This was very nearly successful; in many areas well over 90 per cent of the rabbit population was destroyed. It looked for a time as if the level would fall so low that the animal would indeed become extinct over wide areas. However, in Britain at least, it became apparent that the disease was not hitting all the population, because a small percentage was, for some reason, living above ground in nests, rather as hares do. Rabbits, of course, normally live in large crowded warrens underground and, as the transmitting agent of the disease in Britain is the rabbit flea, the disease spread fast. Myxomatosis became a very effective agent of selection, favouring those individuals who lived relatively solitary lives above ground—only rarely did they catch each other's fleas, and thus each other's disease. (Under normal conditions these rabbits were probably less successful, this open-air habit leaving them more at risk from predators.) Thus individuals who were not necessarily physiologically resistant, but whose behaviour protected them to a considerable degree, contributed to something of a rally in the rabbit population.

In the Australian rabbit population, it appears that a genetically resistant strain emerged after the initial epidemics. The investigation set out in Table 4 was undertaken on rabbits from the Lake Orana district. Precautions were taken to ensure that none of the rabbits tested could have acquired immunity through having survived the disease (in the same way as you may have an immunity to measles as a result of having had it in childhood) or by receiving a temporary 'inoculation' against it from the mother's bloodstream before it was born.

To make sure that the change was in the rabbits and not in the virus (see below), the virus used was from the original outbreak. It was stored, and each year some of it was tested on laboratory rabbits to confirm that its virulence had not declined.

TABLE 4 An investigation showing the emergence of a strain of rabbits resistant to myxomatosis

Test rabbits taken from the wild population		No. of epidemics of myxomatosis previously suffered by the population	Symptoms (%) fatal	moderate	mild
before the arrival of myxomatosis		0	93	5	2
in 1953	after the arrival of myxomatosis	2	95	5	0
in 1954		3	93	5	2
in 1955		4	61	26	13
in 1956		5	75	14	11
in 1958		7	54	16	30

In Britain, although the mortality declined in the later epidemics, there seems to be no evidence that this was due to a genetic change in the rabbits. Apparently, a mutation occurred in the virus that made it much less often lethal to the rabbit. This quite frequently happens with disease-producing organisms, and because such a mutation is advantageous to the organism, the mutant form is likely to become the predominant strain. (Clearly a pathogen that kills its host too soon commits suicide; whereas if a balance can be struck, the pathogen can remain in the population indefinitely.) If the victims of the pathogen survive an attack they will acquire a degree of immunity to it; and if this happens to many individuals, even an epidemic of the original strain will probably not kill them, as they will have at least partial immunity to this as well.

The myxomatosis study is illustrated in TV 21.

These examples illustrate clearly two general points, the first being the fundamental one, that selection (here as applied by human beings) will act on variation to produce a suitably adapted population. The second point follows by implication: such adaptation means it is foolish to expect a 'wonder drug' to solve a pest or disease problem indefinitely.

4.2 Fossils and evolution

Even though only a small fraction of all organisms that have lived are preserved as fossils, it is possible to find a few examples that show a full sequence of changes in morphology in a particular sort of organism over long periods of time. One of the best known examples involves the ancestors of present-day horses. The details of their evolution are described in higher-level Earth science Courses, but for our purposes it is sufficient to know that a comparatively complete fossil sequence exists; we show just one feature from this sequence. Present-day horses (and their close relatives the zebras) are remarkable in that each limb bears just a single large digit; the horse's hoof fits on to the end of this (see Figure 14). When the limbs of the earliest fossil horses are examined (horses that lived some 60 million years ago) it is found that each limb carries four large digits. By looking at successively more recent fossil horses, it is possible to see how the size of all but one of these digits has become progressively smaller. Figure 14 shows this sequence. In fact, it is still possible in present-day horses to detect two small fragments of bone lying one on either side of the main digit. These are all that remain of the other digits.

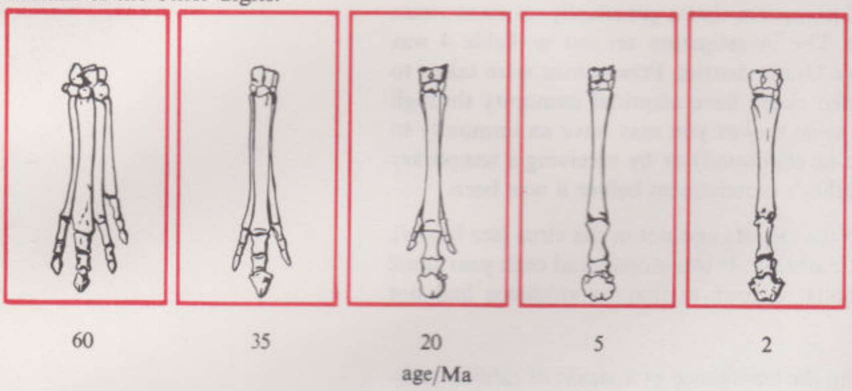


FIGURE 14 Evolutionary changes in the horse's fore-limb.

The example of evolution in the horse is rather atypical, however, by virtue of its completeness. To give an idea of the difficulties that beset palaeontologists trying to trace the progress of evolution by examining the fossil record, let us take an altogether less complete case to look at in detail. A good example for this purpose is the evolution of human beings. It has the added advantage that most people find their own ancestry more interesting than that of other organisms. There are two main purposes behind the material presented in the coming pages. The first is to describe the main features of human evolution insofar as they are known and agreed upon at present. Because new fossils are continually being discovered and there is a good deal of disagreement among specialists of human palaeontology on many of the details of the course of human evolution, this first purpose is perhaps less important than the second, which is to demonstrate that palaeontologists have to make judgments about every fossil that they find, and that their judgments are based upon a number of assumptions.

There are two particularly important judgments that have to be made about a fossil.

1 Judgments about the use to which the fossilized structure was put during the lifetime of its owner

This first kind of judgment can be illustrated by referring to the bones of the pelvis. The shape of the human pelvis is different from that of other primates, and this difference reflects the fact that when human beings stand and move about, they do so in an upright posture, on two legs, whereas other primates spend most of their time moving about on four limbs.

> Look at Figure 15 and read the caption. What is the most distinctive difference between the shape of the pelvic bones of humans and apes? How is this related to their posture?
>
> In humans the ilium is short and wide, forming a sort of dish supporting the internal organs of the abdomen. In apes, by contrast, the ilium is longer and narrower. The different shapes are associated with the different ways in which the bones support the body and the different ways in which muscles act upon the bones (Figure 16).

If palaeontologists find a fossil pelvis looking like Figure 15a they judge that the creature to whom it belonged, like the gorilla and the chimpanzee, usually moved about on four legs, that is, quadrupedally. If the pelvis looks like Figure 15b, however, they judge that its owner habitually went about in an upright posture, that is, bipedally, just like present-day human beings. It is worth underlining the important assumption upon which such judgments are based. If a fossil is found that has certain morphological features that are similar to those of a present-day animal, then it is assumed that in both animals the features play the same role and are adaptations to similar circumstances. This assumption is known as the principle of uniformitarianism, which states that the present is the key to the past, and is discussed in more detail in Unit 26.

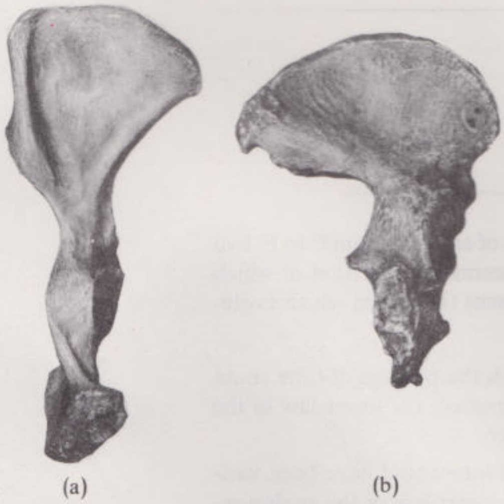


FIGURE 15 The pelvic bone (one half of the complete pelvic skeleton) of (a) a chimpanzee and (b) a modern man. Notice that the upper part of the bone is called the ilium (pronounced either ill-ee-um, or eye-lee-um).

As soon as this assumption is made it becomes possible to infer a great deal about the sort of life led by animals that are known to palaeontologists through even the most fragmentary fossil remains. All that has to be done is to compare the fossil, whether it is a tooth, a limb bone or part of a foot, with a comparable or nearly comparable structure in a living animal, and then examine the way of life of the living animal. For example, if the tooth from the fossil resembles that of a rabbit, then because rabbits eat grass it is likely that the original owner of the fossil tooth ate grass too; if the fossil foot resembles that of a mole, then probably the animal that was fossilized lived underground, or at least spent a lot of its time digging, and so on.

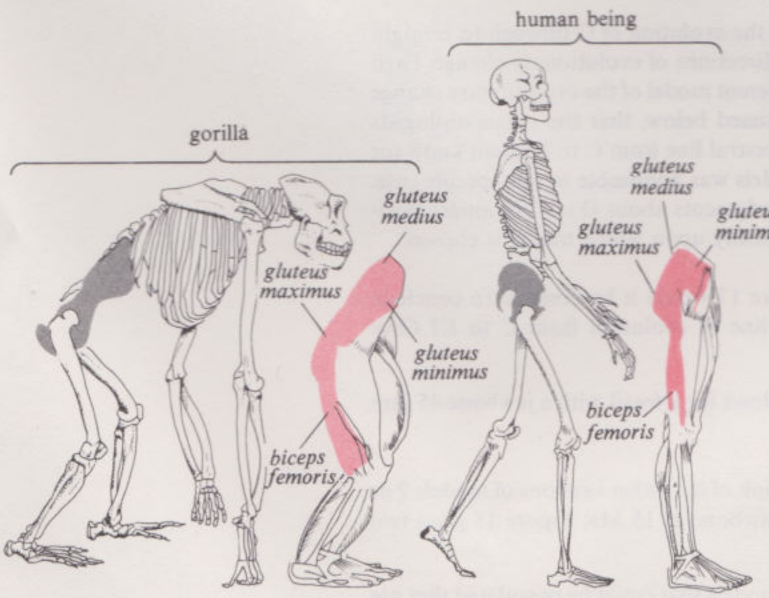


FIGURE 16 Skeletons and leg muscles in a gorilla and a man. (The names of the muscles need not be memorized: they make it easier to compare the two species, however.)

2 Judgments about the evolutionary relationships between fossil organisms

When a fossil is newly discovered, one of the main tasks that palaeontologists set themselves is to assess where it fits in the fossil record. Is it identical or closely related to some previously discovered fossil? Does it perhaps fill a gap in the fossil record between an old fossil and a more recent one descended from it? It is only

possible to answer questions such as these sensibly if something is known about the general trend of evolutionary change that occurred during the period when the fossilized organism was alive, and also if something is known about the rate at which this evolutionary change took place.

To make this less abstract, consider three mammalian skulls, C, D, and E, listed in Table 5. C is known to be the ancestor of E. Skull D has many morphological features similar to those of both C and E.

TABLE 5 Data on three hypothetical fossil skulls

	Skull C	Skull D	Skull E
age (millions of years)	20	15	10
length of lower jaw (mm)	40	45	50

In order to be able to decide whether D is on the line of ancestry from C to E, two pieces of information have to be available. One concerns the direction in which evolution has occurred from C to E, the other concerns the rate at which evolution has occurred. There are several possibilities.

(*a*) *Direction* (i) The change in morphology with the passage of time could have been always in one direction, that is, as time passed, the lower jaw in the evolutionary line from C to E became steadily longer.

(ii) The change in morphology with the passage of time could have been variable in direction. For example, from 20 to 15 Ma the lower jaw in the evolutionary line from C to E could have become shorter, and from 15 to 10 Ma it could have become longer.

(*b*) *Rate* (i) The rate of change in morphological features could have remained constant with the passage of time.

(ii) The rate could have varied as time passed.

There are plenty of examples from the fossil record of changes both in the rate and in the direction of evolution. Indeed, there are examples where a change in the rate of evolution can be so rapid as to give the appearance in the fossil record of a discontinuous jump rather than a continuous change.

Refer now to Figure 17, which shows how the evolution of C through to E might have proceeded under different rates and directions of evolutionary change. Each of the graphs in Figure 17 represents a different model of the evolutionary change from C to E. It may be, and this is discussed below, that the palaeontologists trying to decide whether D was on the ancestral line from C to E might know (or have a very good idea) which of these models was applicable in this specific case. The important thing to note is that any judgments about D's evolutionary position with respect to C and E depends critically upon which model is chosen.

> Under which of the models in Figure 17 would it be possible to conclude that fossil D was directly on the line of evolution from C to E? Give reasons.
>
> Model 1 only. None of the others allows for a fossil with a jawbone 45 mm long to be present at 15 Ma.

This is not to say that it is impossible to think of any other versions of models 2 or 3 that would give a fossil with a 45 mm jawbone at 15 Ma. Figure 18 gives two such examples.

In fact, there is no limit to the number of models that could be postulated that are consistent with D's being on the line of ancestry from C to E. The key question that has to be answered, therefore, is which model to choose.

Sometimes, information is available from other fossils that helps the palaeontologist to make a choice. For example, if the fossils under examination come from a long series whose ages are well known, it may be possible to gain an idea of the rate and direction of evolutionary change in the series as a whole. For example,

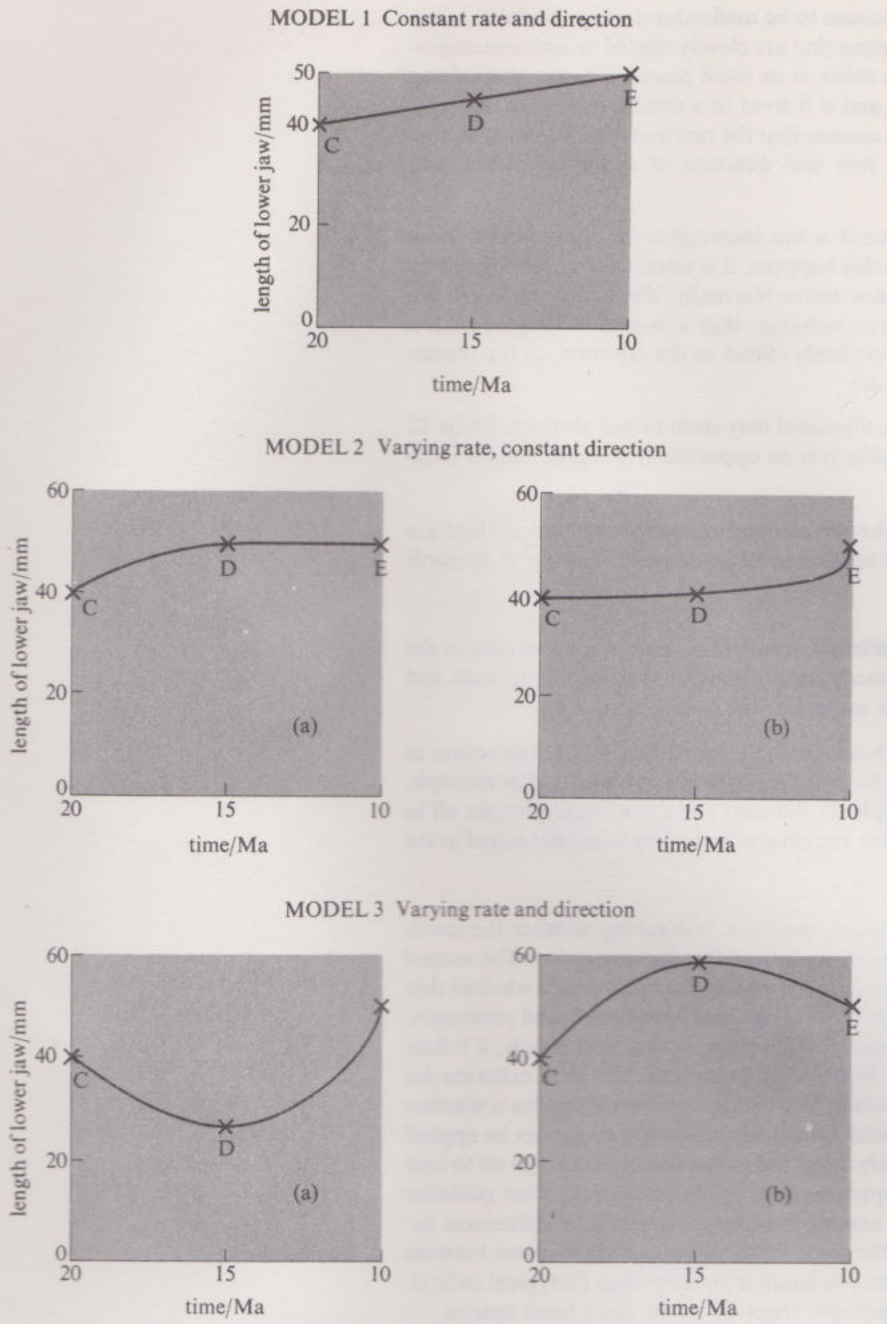


FIGURE 17 Different models for the evolution of C into E.

suppose C and E were part of a long series of fossils A → B → C ——→ E → F → G → H. If the trend throughout the entire series were towards an increase in the length of the lower jaw and if the rate of change in length with time were constant, then it would be reasonable to assume that during the course of evolution from C to E, the rate and direction of evolutionary change would also remain constant.

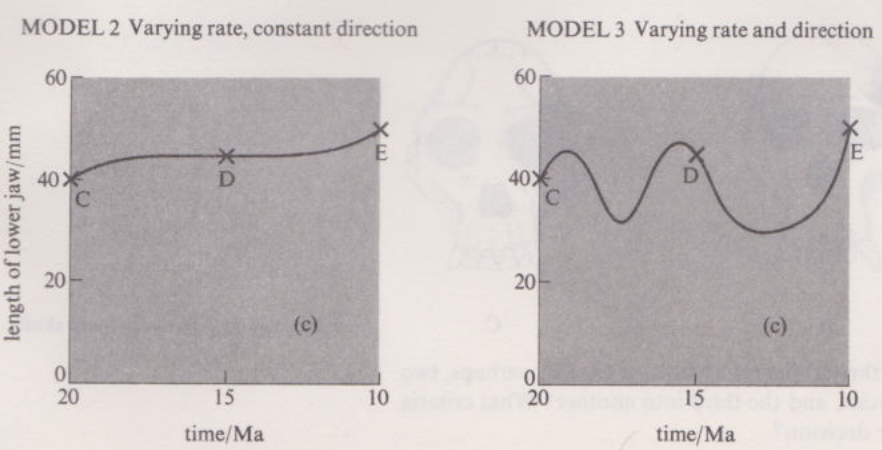


FIGURE 18 Two more models of the course of evolution from C to E.

Another thing that may allow a decision to be made about which model to adopt is the pattern of evolution in organisms that are closely related to and contemporary with C and E. If such a group exists, if its fossil record is better studied and understood than that of C and E, and if it lived in a similar habitat to that of C and E, then it may be justifiable to assume that the rate and direction of evolution from C to E was similar to the rate and direction of evolution in the contemporary group.

Frequently, however, the fossil record is too incomplete for either of the above comparisons to be possible. When this happens, it is usual to choose the simplest model consistent with what evidence exists. Normally, this is the model of constant rate and direction of evolutionary change, that is, model 1 in Figure 17. It is this model that is adopted, unless explicitly stated to the contrary, in the discussion of human evolution that follows.

The two kinds of judgment we have discussed may seem rather abstract. SAQs 12 and 13 at the end of this Section give you an opportunity to make similar judgments about fossil data.

Quite apart from having to make the two assumptions we have outlined, there are other hazards to be overcome if a fossil is to be interpreted sensibly. It is worth mentioning two of them here.

If a collection of fossils of different animals and plants are all found in the same place, does this necessarily mean that they come from animals and plants that all lived together as part of the same community?

No. The fossils might have been carried great distances over the course of millions of years, and might have come together fortuitously. For example, fossils originating from completely different parts of a country might all be washed downstream by a river system and end up by being deposited in the same area.

One difficulty that has to be overcome, therefore, is deciding whether the fossils found together in a group came from organisms that lived together. The second difficulty is that when a fossil is found a palaeontologist must decide whether that fossil belongs to the same species as other fossils that have been found previously. If it does, the fossil is given the same scientific name as the other fossils; if it does not, it is given a different name. With living organisms, the ideal criterion for deciding whether two organisms belong to the same or different species is whether they are able to interbreed in the wild. Obviously, this criterion cannot be applied to fossils, and this means that the only thing that palaeontologists can go on to help them make their decision is the appearance of the fossil remains. One guideline that palaeontologists follow is to assume that the morphological differences between fossil species should be of the same order of magnitude as those between living species. Fossils that differ from one another no more than do typical individuals of a present-day species are grouped together in the same fossil species.

The detailed appearance of the fossils can nowadays be analysed by a number of mathematical techniques going under the name of 'multivariate analysis'; but the palaeontologist still has to make some sort of subjective judgment about whether two or more fossils belong to the same species.

Examine now Figure 19. The three skulls are obviously rather different.

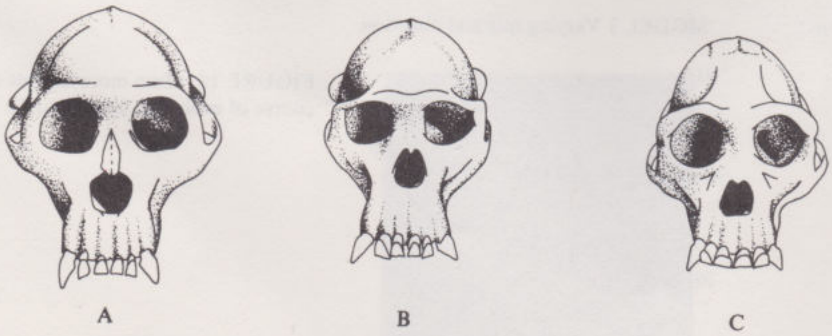


FIGURE 19 Three primate skulls.

Should they be assigned to three different species, or should, perhaps, two of them be put into one species, and the third into another? What criteria are you using to make your decision?

On the basis of size it might seem reasonable to put skulls B and C together in one species, and A on its own into another. On the basis of the shape of the ridge of bone surrounding the eyes, however, A and C might be grouped together with B left on its own. In fact, neither interpretation is correct. All three skulls are from present-day adult chimpanzees, all from the same local population. The differences in the skulls simply reflect the differences among the adult individuals in that population. This rather well known example was put forward by the palaeontologist Elwyn Simons to serve as a warning against erecting large numbers of new species on the basis of minor differences in fossil morphology. The necessity for this warning is only too clear when it is realized that there may be quite substantial differences in the skeletons of males and females of the same species, and in the skeletons of immature and mature animals. It has not been unknown in the history of palaeontology for the male and female of the same kind of animal to be identified as completely different species.

Armed with the knowledge of some of the assumptions that palaeontologists make when they interpret their fossil finds, and warned about some of the pitfalls that they face, it is now possible for us to discover what is currently known about the ancestry of the human race.

Study guide for Sections 4.3 and 4.4

The remainder of this Unit is devoted to a discussion of the ancestry of the human race. As one of the main difficulties that palaeontologists face is deciding where newly discovered fossils fit into an evolutionary framework, we shall confront you with some of the problems and get you to work them out for yourself. In Section 4.3 some of the most important fossil finds known to scientists at the beginning of the 1970s are described together with the way in which they were, at that time, thought to fit into an evolutionary sequence.

Throughout the 1970s there have been several important fossil hominid discoveries. Information on each major fossil discovery—for example, its location, its age, the parts of the skeleton that were found—is printed on a separate card. In Section 4.4 you will meet the same problem that faced palaeontologists when these discoveries came to light: they do not fit into the evolutionary scheme that was accepted at the beginning of the 1970s. You will be asked to try to devise a new scheme that accommodates the new finds. The answer to question 6 of this Exercise summarizes how these more recent discoveries may fit into the evolutionary sequence that led up to modern human beings.

Before reading on, you may find it helpful to refer again to Figure 6, which shows the taxonomic relationships of human beings and other primates. Figure 6 is on p. 13.

4.3 Human evolution: the view current in the early 1970s

Refer first to Figure 22, which shows the possible evolutionary relationships of the specimens described in this Section. The diagram should help you to keep in perspective the material discussed in this Section.

Ramapithecus

The story of human evolution can most conveniently be taken up about 13 million years ago, at a time when an animal called *Ramapithecus* was alive. In 1932 a fragment of an upper jaw was found in northern India that had certain features that were different from the jaws of apes of the same antiquity. The fragment was dated as being somewhere between 11 and 13 million years old. Since 1932 several more fragments of teeth and jaws have been found, and recently some complete lower jaws, aged somewhere between 10 and 8 million years, have been discovered in the Siwalik region of Pakistan. Filmstrip 20.2, Frame 8 (which should be viewed through your stereo viewer) shows one of these lower jaws (centre), viewed from above looking down at the teeth. (Read the labelling in Figure 20; this shows the names given to the different teeth in the primate jaw.) Compare the lower jaw of *Ramapithecus* with the lower jaw of a fossil ape of similar age (top) and with the lower jaw of a modern human being (bottom). Certain interesting features become apparent.

Filmstrip 20.2

teeth in the primate jaw

First, the shape made by the row of teeth is different in the three animals. The human tooth row is almost semi-circular, whereas the teeth of the fossil ape, like those of living apes, run back from the front of the jaw in two nearly parallel rows. *Ramapithecus* is intermediate; the tooth row is V-shaped. This suggests that *Ramapithecus* has begun to move away from the arrangement of teeth in the early ape towards that found in human beings.

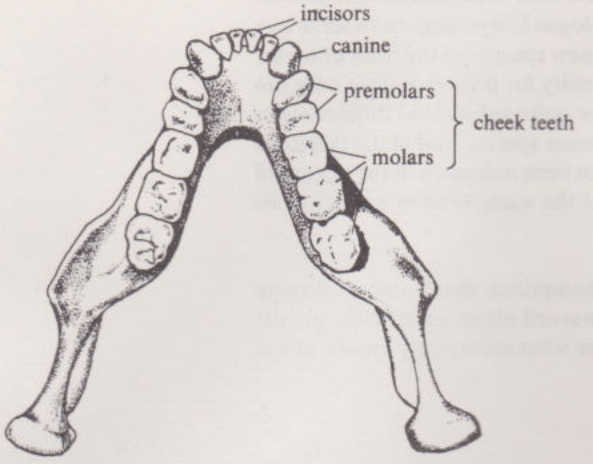


FIGURE 20 The lower jaw of a primate (*Ramapithecus*) to show the different kinds of teeth.

Another feature in which *Ramapithecus* differs from both living and fossil apes is in the hard layer of enamel that covers the teeth. In the apes the layer that covers the cheek teeth is thin, and becomes worn away as the animal ages. In *Ramapithecus* the enamel layer is much thicker—up to 2.5 or 3 mm thick in some specimens—and in this respect *Ramapithecus* resembles more recent fossils that are definitely human.

The existence of this thick enamel layer on the cheek teeth suggests, by analogy with present-day mammals, that *Ramapithecus* fed on grass or on other tough food such as nuts or roots, unlike the fossil apes, which lived in forest and fed on soft food such as fruits and shoots. It is possible, therefore, that some time between 13 and 8 million years ago *Ramapithecus* (and other animals like it) left the forests in which their ancestors lived, and took up a life in areas of woodland, that is, in areas intermediate between forest and open country. It is from this group of animals that human beings ultimately descended.

> Is it possible to tell from the jaws and teeth whether *Ramapithecus* was bipedal? If not, what other parts of the skeleton would be needed?
>
> Unfortunately, it is not. Any one of several parts of the body would indicate that *Ramapithecus* was bipedal, but these are all missing. For example, the shape of the pelvis would give the necessary information.

Because bipedalism is one of the main hallmarks of the hominids, it is particularly frustrating that this evidence is lacking. It is therefore necessary to turn to more recent fossils, to see how closely they resemble present-day human beings. Unfortunately, this leads to a still bigger source of frustration: from 8 million years ago, which is the date for the most recent *Ramapithecus*, until 3 million years ago there is a tantalizing gap; and only the most unsatisfactory fragments of fossil material have been discovered so far (Figure 22). Fossil hominids that are less than 3 million years old are less fragmentary, and it is these that we shall discuss in some detail.

In 1925, a South African anatomist, Raymond Dart, discovered the fossilized skull of an animal that had some remarkably human features, and yet was clearly not itself a member of the human species, *Homo sapiens*. It turned out to be the skull of a young animal, and because it was discovered near the town of Taung in Botswana, it has come to be known as the Taung child. Since then, there have been numerous other finds of adult specimens, whose features are sufficiently similar to those of the Taung child for it to be clear that they belong to the same species. Dart called this animal *Australopithecus* (which literally means southern ape). It is very difficult to give an accurate date for the *Australopithecus* fossils found in South Africa, but they are generally thought to be about 2–3 million years old. However, specimens of *Australopithecus* have also been discovered in the 1960s in Olduvai Gorge in East Africa by Louis and Mary Leakey, and it has been possible

Australopithecus

to date them accurately: different specimens range in date from nearly 2 to 1.5 Ma. It has become clear that there are two main sorts of *Australopithecus*, one with a heavily built skull and skeleton and the other much more slender. The former is called *Australopithecus robustus*, for obvious reasons, and a skull is shown on the right in Filmstrip 20.2, Frame 9. (One particularly well built specimen, endowed with a formidable set of teeth, was nicknamed 'Nutcracker Man'.) The more delicately built species is called *Australopithecus africanus*, shown in Filmstrip 20.2, Frame 9 (on the left). The picture shows what the skull of one particularly complete *A. africanus* specimen looks like when viewed from the side, and what the lower jaw looks like when viewed from above, looking down on the teeth. Front views of the two specimens are shown in Figure 21.

Filmstrip 20.2

FIGURE 21 Skulls of *A. africanus* (left) and *A. robustus* (right).

How does the shape of the tooth row of *A. africanus* compare with that of *Ramapithecus* and *Homo sapiens* (Filmstrip 20.2, Frame 8)?

Filmstrip 20.2

The tooth row of *A. africanus* is intermediate between that of *Ramapithecus* and *Homo sapiens*: it is rather rounded in appearance, and the teeth diverge more strongly towards the back than they do in *Ramapithecus*. What is more, the teeth of *A. africanus* are rather more uniform in appearance than they are in *Ramapithecus*. The canine teeth are quite stout and short in comparison with those of *Ramapithecus*.

After the fragmentary *Ramapithecus* material, it is a relief to have such complete specimens with which to work. Filmstrip 20.2, Frame 9, shows that *A. africanus* had a skull whose top was round and smooth, like a human one. It is possible to estimate roughly how large the brain was, and these estimates run from 450 to 600 cm^3. This is about the same size as the brain of a chimpanzee, but very much smaller than the 1 450 cm^3 for *Homo sapiens*. Although absolute brain size is not a reliable indicator of the complexity of the brain's structure or of the animal's behavioural and intellectual abilities, this difference does suggest that *Australopithecus* still had a long way to go to match *Homo sapiens*.

Important though these features are, there is another which makes it possible to infer whether or not *Australopithecus* had acquired one of the key features of hominids, namely a bipedal posture. Look at Filmstrip 20.2, Frame 10, which shows half of the pelvis of a chimpanzee (left), of *Australopithecus* (centre) and of *Homo sapiens* (right). The pelvis of *Australopithecus* resembles that of *Homo sapiens* closely. Both have a broad, flat plate of bone at the top, and a short, narrow part pointing downwards, whereas the chimpanzee has a less widely flared upper end, and a rather longer, stouter, downward-pointing part. This suggests that *Australopithecus*, like modern human beings, was habitually bipedal.

Filmstrip 20.2

As we have mentioned, the *Australopithecus* specimens collected from Olduvai Gorge, Tanzania, could be dated quite accurately. Close examination of these specimens revealed not only that there were robust and slender forms, but also that some of the slender forms appeared to differ in several ways from the slender *A. africanus* specimens discovered in South Africa. The cheek teeth of the slender form from Tanzania were smaller (Filmstrip 20.2, Frame 11) and the incisors larger than those of *A. africanus* and more like those of humans. What is more, relative to its body size, it had a considerably bigger brain, 600–800 cm^3, in comparison with the 450–600 cm^3 of *A. africanus*. Especially important is the fact that the specimens were found at sites that yielded large numbers of simple stone tools, such as flakes and choppers (Filmstrip 20.3, Frame 12). Because of these

Filmstrip 20.2

Filmstrip 20.3

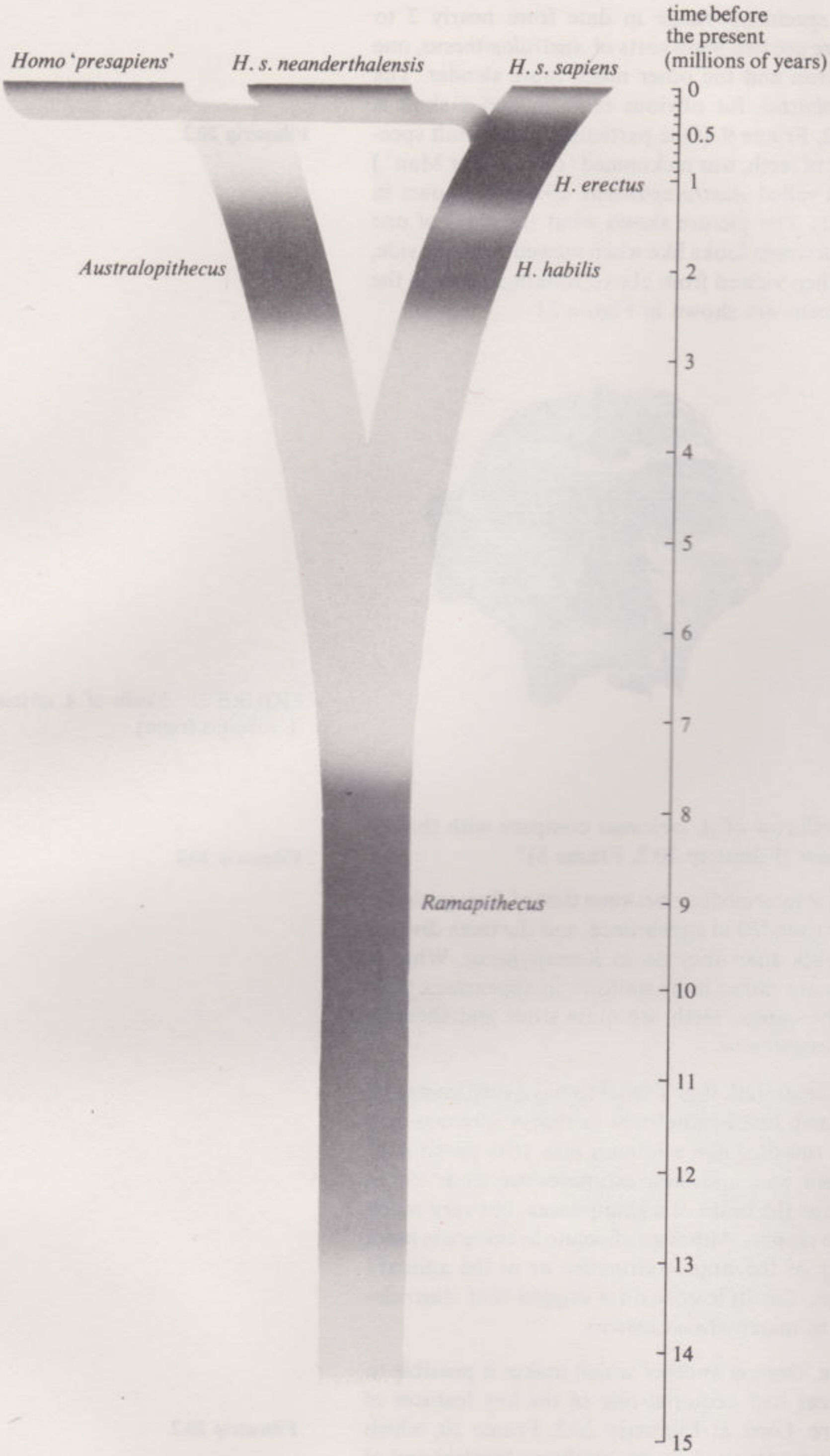


FIGURE 22 Tentative evolutionary relationships of hominoid fossils, based on information available by the end of the 1960s.

tools, the specimen was called *Homo habilis* (which means 'handy man'). It is clear from the broken bones of other animals found at the same site that *Homo habilis* hunted, butchered and ate animals, a new and significant development in behavioural evolution.

Homo habilis

There has been some disagreement over whether *Homo habilis* is sufficiently human to be included within the genus *Homo*, or whether it is no more than an advanced *Australopithecus*. Because it has a larger brain and more human teeth than *A. africanus* it seems reasonable to include *H. habilis* within the genus *Homo*, and this is the practice adopted in this Unit. Whichever viewpoint one adopts, *H. habilis* and *A. africanus* are direct contemporaries; hence, *A. africanus* is very unlikely to have been the ancestor of *H. habilis*, and therefore the direct ancestor of human beings (see Figure 22).

The next major step in the evolutionary progress towards modern human beings is represented by a fossil that carries still further the trends seen in *Homo habilis*. This fossil is called *Homo erectus*, and it has a still larger brain-case and still smaller cheek teeth than *Homo habilis*. It gains its name *erectus* from the fact that

Homo erectus

the shape of its pelvis and skull indicate that it was completely bipedal. *H. erectus* lived more recently than *H. habilis* (although it was a contemporary of the last of the *Australopithecus* population), and it seems to fit well on the direct line of descent from *H. habilis* through to modern human beings (Figure 22).

The first specimens of *Homo erectus* to be discovered were found in Java and in China, not far from Peking. Since then other specimens have been discovered in Europe and Africa. The oldest specimens are probably about one and three-quarter million years old, and the youngest about 500 000 years old. Look at Filmstrip 20.3, Frames 13 and 14, which show the skull of one of the Chinese specimens (*Peking Man*), which is one of the most recent (the age and the origin of the specimen are important, because there are certain variations in morphology). The skull has a rounded row of teeth, and the teeth are fairly uniform. By far the most spectacular advance over *Australopithecus* and *H. habilis*, however (and this is what qualifies it as an undoubted member of the genus *Homo*), is the very much bigger brain. The brain size is nearly up to that of *Homo sapiens*. It ranges, from early to late specimens, from 775 to 1 100 cm^3, whereas *Homo sapiens* brains average 1 450 cm^3. As the early *H. erectus* specimens lived a little over a million years before the late ones, this means that a huge increase in brain size occurred over what, in terms of evolutionary history, is a very short time indeed (Figure 23).

Filmstrip 20.3 Peking Man

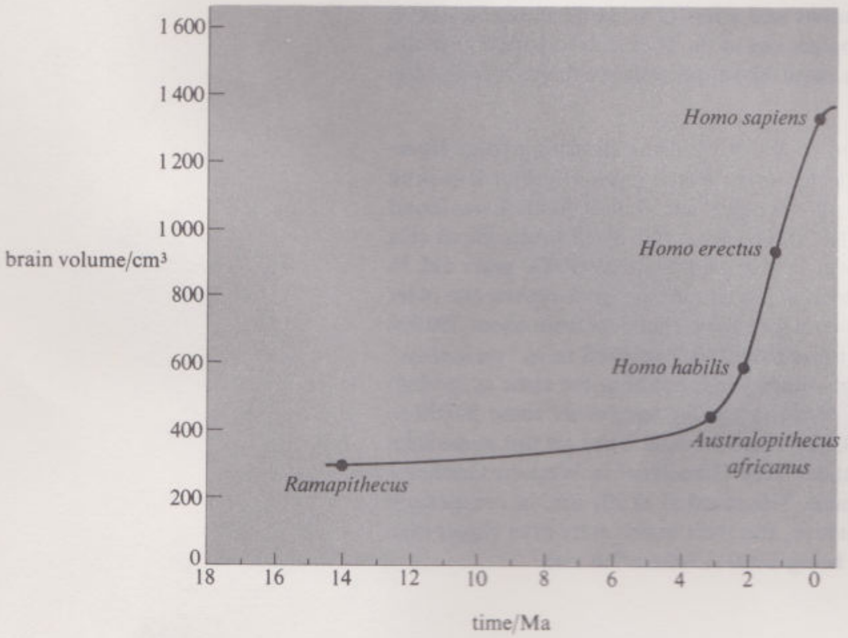


FIGURE 23 Increase in brain size during hominoid evolution.

Homo erectus was also a tool-maker. The sites where fossils of these species are found often yield up stone tools, together with the remains of animal bones that have been split and broken by these tools. On this evidence, Peking Man must have been a big-game hunter and, because indications of ashes and hearths have been found, must also have discovered the use of fire. All of this is evidence of advances in the species' behaviour, and such advances must, of course, be a correlate of its big brain.

The story of hominid evolution as outlined here shows that the teeth and bodily posture of fossil hominids began to evolve towards a modern human condition much earlier than did their brains. This raises both an important point and an interesting question. The point is that not all of the features of an animal change at equal rates over the course of evolution; some features change sooner than others. This unequal rate of advance is called *mosaic evolution*. And the interesting question is this.

mosaic evolution

If you were to find a fossil hominid, contemporary with *Australopithecus* but with a human-sized brain and ape-like jaws, what would be your reaction?

It should be one of extreme suspicion. In fact, just such a specimen did turn up in the guise of the infamous Piltdown Man. This turned out to be a forgery, consisting of a human skull and the lower jaw of an orang utan, stained and battered to make them both look ancient, and then planted in

an area of a suitable antiquity. As the specimen was planted before any *Australopithecus* or *Homo erectus* specimens had been discovered, it was regarded as authentic and misled people for decades until finally revealed as an imposter.

The most recent *Homo erectus* specimens are about 500 000 years old. After that there is a gap of about 100 000 years before any other hominid fossils are found. From 200 000 years ago until the present there are numerous fossil finds of human beings, mostly from Europe. As these fossils are very recent compared with those of the earliest human ancestors, and as they have been discovered in such numbers from thoroughly worked sites in Europe, it might be expected that the final lap of the story of human evolution would be fully documented and plain-sailing. Sadly, this is not so.

Look at the skulls in Filmstrip 20.3, Frame 15. (These are also reproduced as Figure 24.) Compare skulls A and B with that of *Homo sapiens* (C).

Filmstrip 20.3

Ignoring for the moment the size of the skulls, which of the two appears to be more like that of *Homo sapiens* in shape?

Skull A has a more rounded roof than skull B and in this respect is more like *Homo sapiens*. It also bears a closer resemblance in that it has smaller ridges of bone above the eyebrows and a less protruding snout. Skull B is flatter than the other two; it bulges out at the back and the upper jaw and nose project forwards, giving a snout-like appearance to the face. It also has heavy ridges above the eyes.

It would make for a tidy conclusion to the story if the transition from *Homo erectus* to *Homo sapiens* ran through the series, *Homo erectus* → skull B → skull A → *Homo sapiens*. Unfortunately, skull A is older than skull B. Skull A was found in Steinheim in Germany, and is about 200 000 years old. Skull B was found at la Ferrassie near Périgueux in south-west France and is about 60 000 years old. In other words, the more recent specimen is *less* like *Homo sapiens* than the older one. The Steinheim skull is one of several specimens that date from about 200 000 years ago; these specimens are sometimes collectively referred to as '*presapiens*'. Their brains were about 1 325 cm^3 in volume; that is, about the same as modern man. The la Ferrassie skull is one of many similar specimens some 50 000 to 70 000 years old that are collectively called Neanderthals. They get this name from a site in the valley of the river Neander near Düsseldorf in Western Germany, which has yielded up many specimens. Neanderthal skulls are, in comparison with modern human skulls, quite massive, and their brains were even bigger than those of present-day *Homo sapiens*, being 1 300–1 700 cm^3 in size.

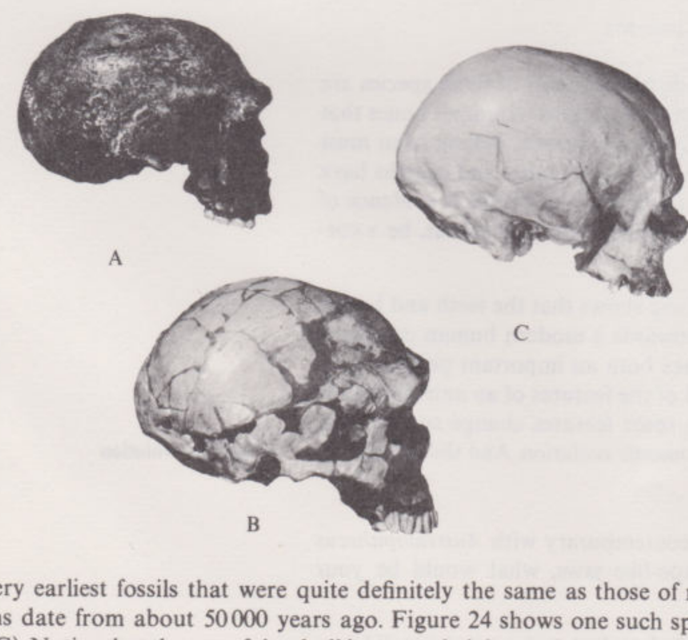


FIGURE 24 Skulls of recent hominids.

The very earliest fossils that were quite definitely the same as those of modern humans date from about 50 000 years ago. Figure 24 shows one such specimen (skull C). Notice that the top of the skull is a rounded dome, that there is a vertical forehead, that there are no eyebrow ridges and that the facial region below the eyes is vertical, rather than sloping forward. Filmstrip 20.4, Frame 16, shows the lateral view of the lower jaw of a modern human being.

Filmstrip 20.4

What feature that is absent from any of the other hominids described so far does this lower jaw possess?

A chin. The chin is one of the most distinctive features of the modern human skeleton. The lower jaw of many other primate species is strengthened by a thickening on the inside at the front. The human jaw has the thickening on the outside, and it is this curious feature that contributes strongly to the humanness of the human face.

Cro-Magnon Man

These early fossils that are identical to modern humans are known collectively as *Cro-Magnon Man*. They were direct contemporaries of Neanderthal Man in Europe, so Cro-Magnon Man cannot have evolved from the Neanderthals there. However, other fossil hominids that possess a mixture of Cro-Magnon and Neanderthal features have been found elsewhere. With all these complications, it is only possible to speculate about the course that evolution took from *Homo erectus* to present-day humans.

One such speculation runs like this. *Homo erectus* may have given rise, in different parts of the world and at different times, to a variety of different sorts of hominid, each kind differing from the next in details of the size, shape and robustness of the skull, and also in details of other parts of the anatomy. At a time when the more northerly parts of Europe and Asia were going through alternating cold (the Ice Ages) and warm periods, parts of Asia and Africa were consistently warm, and the '*presapiens*' type may have appeared and lived in these areas. The Neanderthals lived in northern Europe, even during the Ice Ages, and so must have had a pretty rugged life; it is possible that some of the different groups of '*presapiens*' migrated north to these colder regions from time to time.

About 50 000 years ago, a final invasion from the south into Europe took place, this time of Cro-Magnon Man, who perhaps migrated northwards there from the warmer parts of Asia. Within a few thousand years of this, Neanderthal Man and all of the other northern variants had vanished, leaving only Cro-Magnon Man. It could be that Cro-Magnon Man killed off the Neanderthals, but a less melodramatic explanation would be that the Cro-Magnon population reproduced more successfully, that they interbred to some extent with the Neanderthals, and that the numbers of Neanderthals dwindled. If this is so, then it is quite possible that there is a fair sprinkling of Neanderthal genes still present in today's human population. The evidence that Cro-Magnon and Neanderthal Man may have formed interbreeding populations comes from the discovery of a site on Mount Carmel where specimens intermediate between Cro-Magnon and Neanderthal Man have been found. Whether they interbred or not (and the evidence is still disputed) Neanderthal and Cro-Magnon Man are sufficiently similar in appearance for palaeontologists to place them in the same species, *Homo sapiens*. The two are distinguished in their names by adding a third name to each, the subspecific name. Neanderthal Man is called *Homo sapiens neanderthalensis*, and Cro-Magnon and present-day humans are called *Homo sapiens sapiens*.

Homo sapiens neanderthalensis
Homo sapiens sapiens

This completes the picture of hominoid evolution as it was known at the beginning of the 1970s. Since 1970 a number of important fossils have been discovered that have filled in several gaps in the record, and also have made it necessary to reconsider the evolutionary position of the fossils shown in Figure 22. These more recent fossil discoveries are described in Exercise 2.

4.4 Exercise 2 Making sense of recent discoveries

Each of the cards 1–4 accompanying this Unit gives details of a different fossil discovered since 1970. Each card gives information on when the fossil was discovered, on some of its most important morphological features and its age. Several of the sites where fossils were discovered are shown in Figure 25 (overleaf).

Read the information on the cards and then answer questions 1–6. Attempt all six questions before turning to the answers on p. 44. Questions 1–5 should help you to formulate ideas about how the fossils fit into the evolutionary record. In question 6, you are asked to construct a new evolutionary tree that incorporates these new fossils together with the fossils shown in Figure 22. You will find that Figure 22 will have to be modified in certain respects for this to be achieved. The

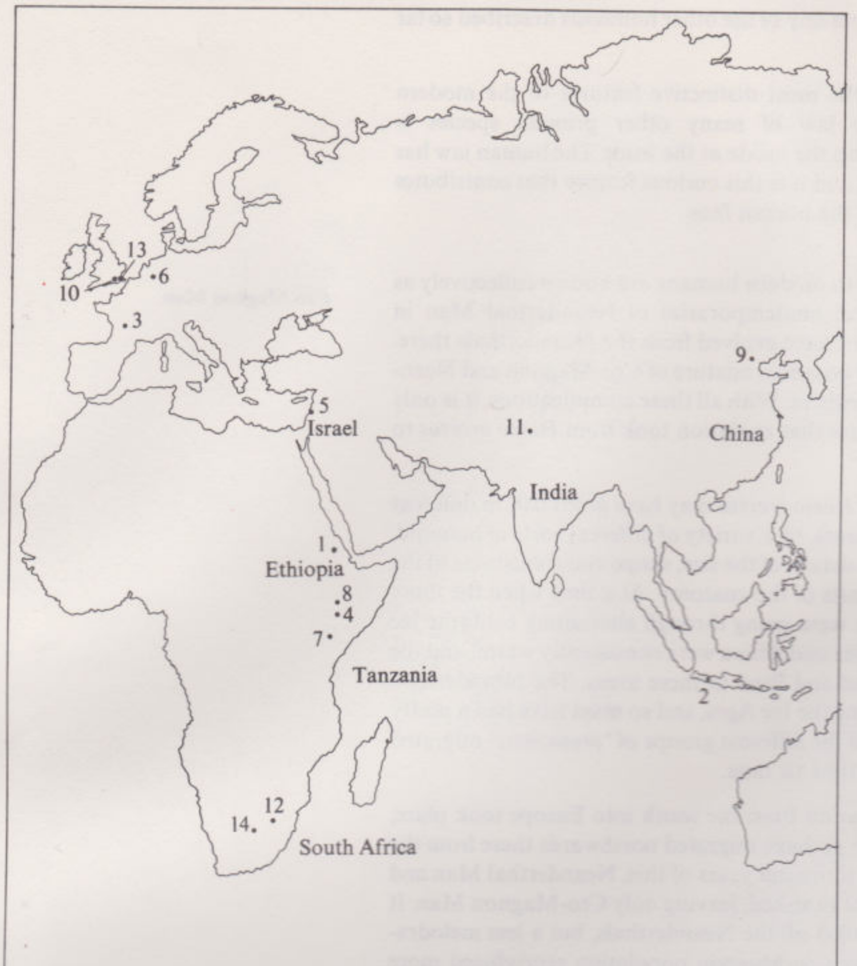


FIGURE 25 Major human and pre-human fossil sites mentioned in this Unit.

1 Hadar	8 Omo
2 Java site	9 Peking Man
3 La Ferrassie	10 Piltdown (discredited)
4 Lake Rudolph & Koobi Fora	11 Siwalik Hills
5 Mt. Carmel	12 Sterkfontein
6 Neanderthal Man	13 Swanscombe
7 Olduvai Gorge & Laetolil	14 Taung

reason for having the information about the recent fossil discoveries on cards is that it allows you to shuffle them around so that you can try out different possible evolutionary trees.

1 In the light of the discovery of 1470 (card 1), is it likely that *Australopithecus africanus* is the direct ancestor of modern human beings? Give reasons.

2 Was Lucy (card 2) bipedal? Give reasons.

3 Compare Lucy's teeth with those of *Ramapithecus* (Filmstrip 20.2, Frame 8) and recent hominids such as *Homo erectus*. What does this comparison, together with your answer to question 2 show about Lucy's evolutionary position?

Filmstrip 20.2

4 Could Lucy have been an ancestor of modern human beings? Give reasons.

5 Why is it important that *Homo erectus* (card 4) has been discovered in East Africa as well as in places like China and Java?

6 Construct an evolutionary tree that incorporates 1470, Lucy, LH2 and 4 (card 3), as well as the fossils mentioned in Figure 22 (p. 34).

4.5 Objectives of Section 4

Now that you have completed this Section, you should be able to:

(a) Distinguish between micro-evolution and macro-evolution.

(b) Make judgments about the way of life of animals by comparing the characteristics of their fossil remains with the characteristics of living animals.

(c) Explain the rationale behind the arrangement of fossils into one particular evolutionary sequence (say, A B C) rather than another (say, B A C).

(d) Recognize the characteristics of the pelvic bones of living and fossil hominoids that indicate whether the animals from which they originate were quadrupedal or bipedal.

(e) Describe the main changes in the shape of the tooth row and in the shape and size of the teeth that occurred during hominoid evolution.

(f) Describe the main changes in brain size that occurred during hominoid evolution.

(g) Given information on the morphological features and age of hominoid fossils, arrange them into a plausible evolutionary sequence.

To test your understanding of this Section, try the following SAQs.

SAQ 10 (a) What distinguishes studies of micro-evolution from macro-evolution?

(b) What conditions are necessary for it to be possible to detect micro-evolutionary change?

SAQ 11 Skull A (Figure 26) belongs to a fossil mammal. Skulls B, C, D and E come from present-day mammals. What sort of life did A probably live? Explain your reasoning.

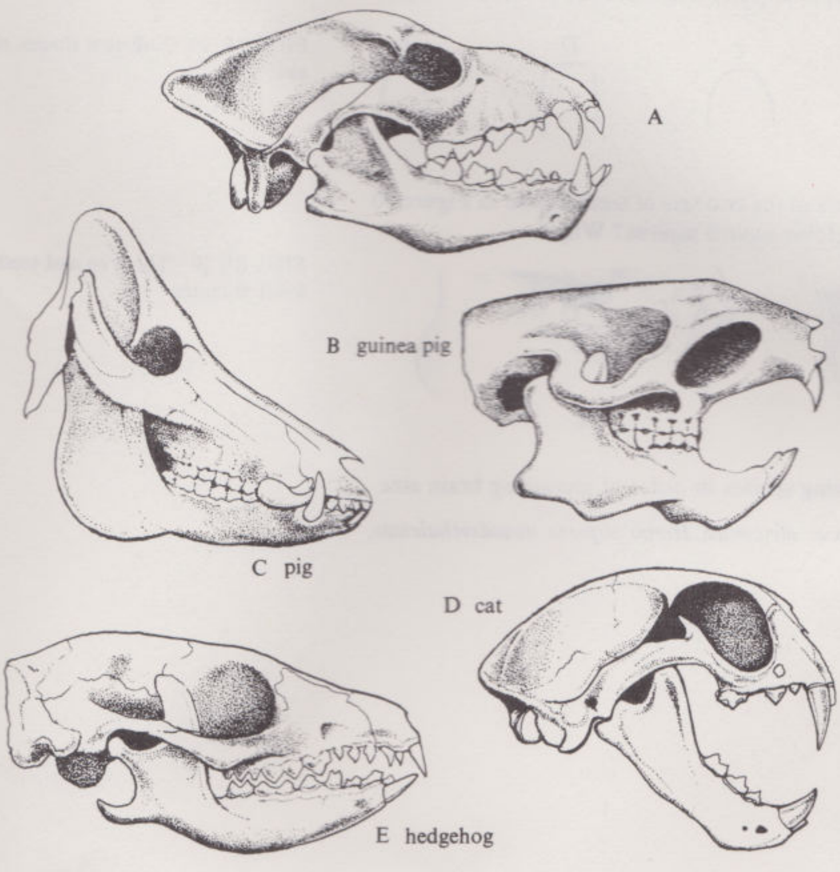


FIGURE 26 Skulls of living and fossil mammals.

SAQ 12 Arrange the bones in Figure 27 into two different evolutionary sequences, using two different models for the direction and rate of evolution. State in each case which model you have chosen. (All bones are hypothetical, but can be assumed to be drawn to the same scale. B is the oldest, D the most recent.)

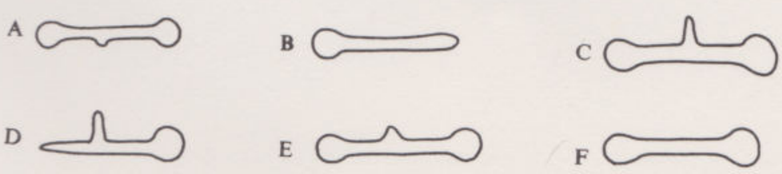


FIGURE 27 Some fossil bones.

SAQ 13 Figure 28 shows the complete pelvic skeleton of a fossil hominid. Was it bipedal or quadrupedal? Give reasons.

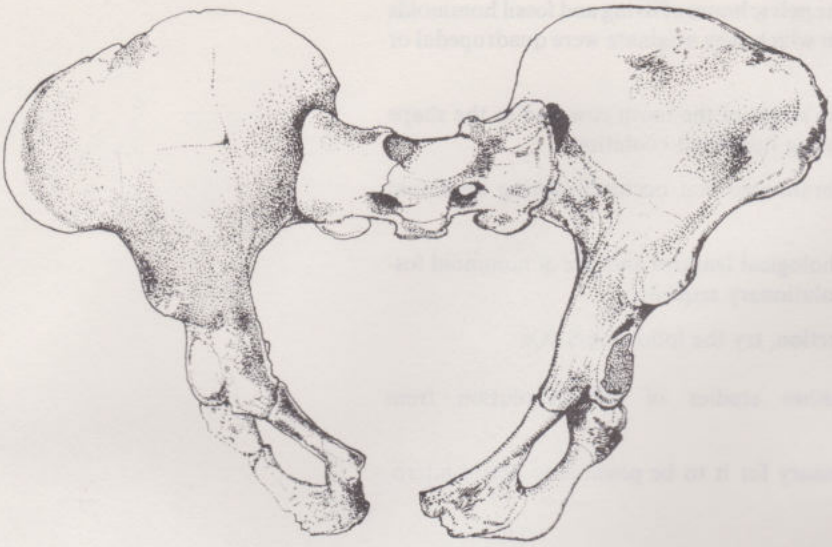


FIGURE 28 The pelvic skeleton of a fossil hominid.

SAQ 14 Which of A to E in Figure 29 would you expect to be typical of the shape of the tooth row (a) of an early hominoid (b) of a late hominid?

FIGURE 29 Different shapes of tooth row.

SAQ 15 Which of the owners of the two sets of teeth shown in Figure 30 was more closely related to *Homo sapiens sapiens*? Why?

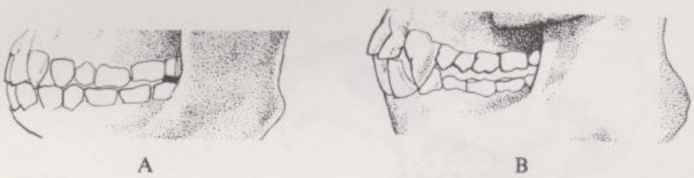


FIGURE 30 The jaws and teeth of two fossil primates.

SAQ 16 Arrange the following species in order of increasing brain size.

Homo erectus, Australopithecus africanus, Homo sapiens neanderthalensis, Homo sapiens sapiens.

Objectives of Unit 20

The Unit's Objectives are virtually identical to the Objectives listed at the end of each Section; they fall into several rather distinct groups. Objectives 1–3 deal with speciation (Section 1); Objectives 4–6 deal with the taxonomic hierarchy (Section 2); Objective 7 deals with adaptive radiation (Section 3); Objectives 8–12 deal with the history of evolutionary change (Section 4).

Now that you have completed this Unit, you should be able to:

1 Give the meaning of the terms 'species' and 'speciation' (*SAQs 1 and 2*).

2 Explain why reproductive isolation is necessary if populations of organisms are to diversify (*SAQ 3*).

3 Explain why geographical and behavioural isolation can result in reproductive isolation (*SAQs 4 and 5*).

4 Draw and interpret an evolutionary tree (*SAQ 6*).

5 Understand the hierarchical principle of taxonomic classification (*SAQ 7*).

6 Remember the terms: phylum, class, order, family, genus, and species; arrange the terms in their correct hierarchical sequence (*SAQ 8*).

7 Understand the meaning of the term 'adaptive radiation', and give an example of it (*SAQ 9*).

8 Distinguish between micro-evolution and macro-evolution (*SAQ 10*).

9 Make inferences about the way of life of animals by comparing the characteristics of their fossil remains with the characteristics of living animals (*SAQ 11*).

10 Explain the rationale behind arranging fossils in one particular evolutionary sequence (say, A B C) rather than another (say, B C A) (*SAQ 12*).

11 Recognize the characteristics of the pelvic bones of living and fossil hominids that indicate whether the animals from which they originated were quadrupedal or bipedal (*SAQ 13*).

12 Describe the main changes in the shape of the tooth row and in the shape and size of the teeth that occurred during hominoid evolution (*SAQs 14 and 15*).

13 Describe the main changes in brain size that occurred during hominoid evolution (*SAQ 16*).

14 Given information on the morphological features and age of hominoid fossils, you should be able to arrange them into a plausible evolutionary sequence (*Exercise 2*).

Objectives 1, 4, 5 and 6 are the ones that will be made most use of in the remaining biology Units of S101, and in higher level biology courses. All of the Objectives are important in the sense that they will be assessed.

SAQ answers and comments

SAQ 1 (*Objective 1*) Not necessarily. The key factor in determining whether two kinds of organism belong to the same species is whether they interbreed to produce fertile offspring *under natural conditions*. If they do, they belong to the same species. If they do not, and come from the same locality, then they do not belong to the same species.

SAQ 2 (*Objective 1*) (i) and (ii) are wrong. If you chose either of these, re-read the Section. (iii) is the definition of speciation given in the Section and is the correct answer. (iv) may have caused you some problems. In fact, it has caused evolutionary biologists a lot of problems too. If two races are geographically so far apart that they can never meet under natural conditions, and yet are clearly similar and perhaps even linked geographically by a series of intermediate races—surely they should be put in the same species? This is where subjective judgment and common sense come in. In this instance, the two races would almost certainly be put in the same species, just as they are, for example in the case of the American song sparrow. On the other hand, if two groups of organisms live so far apart that they can never meet under natural conditions, are not linked geographically by a series of intermediate races and yet are rather similar phenotypically, it is difficult to decide whether they should be put into the same or different species. Again, it is a matter of subjective judgment. It is, in fact, comparatively rare for biologists to be able to apply the criterion of 'interbreeding under natural conditions' to determine whether the organisms they are examining belong to the same or to different species. More often than not they have to base their judgment solely on the phenotypic differences between the organisms under examination and decide for themselves how significant these differences are.

SAQ 3 (*Objective 2*) (iv) is the correct answer. (i) and (iii) are both incorrect for the same reason: they are not explanations at all. They are simply restatements of the question in different words; that is, the question asks, 'Why is reproductive isolation necessary for diversification?' and both (i) and (iii) answer 'because reproductive isolation is necessary for diversification'. This sort of pseudo-explanation is notoriously common in biology. (ii) is wrong in two senses. First, it is not necessarily true that reproductive isolation prevents races from competing with one another. Second, even where it is true, it is not a correct explanation of why reproductive isolation is necessary if populations are to diversify.

SAQ 4 (*Objective 3*) The two species might: (i) be active at different times of the day; (ii) inhabit different parts of the same locality (different species of mosquito, for example, tend to fly at different heights within a forest); (iii) avoid each other if ever they heard, saw or smelt each other; (iv) might be reproductively active at different times of the year.

SAQ 5 (*Objective 3*) (i) The building of roads (particularly motorways) could separate ground-living animals from each other.

(ii) Agricultural practices, for example, the removal of hedgerows could isolate the hedgerow community on one side of a field from the hedgerow community on the other.

SAQ 6 (*Objective 4*) (a) B and C. Their ancestors diverged from each other more recently than any of the other species.

(b) Yes. The ancestors of D and E diverged from each other more recently (at 3) than did those of A and E (at 2).

(c) No. The ancestors of C and D diverged at 2, whereas the ancestors of B and C diverged at 5. Note that the horizontal distance between the letters C and D is not an indicator of how closely related the two species are.

SAQ 7 (*Objective 5*) (a) Yes. A family may contain several genera—see Figure 5 on p. 11.

(b) No. A family is a subset of an order; that is, all of the organisms belonging to one family necessarily belong to the same, much larger, grouping—the order (just as all people living in London necessarily live in England). See Figure 5.

SAQ 8 (*Objective 6*) The corrected version of Table 1 is:

TABLE 1

Hierarchical sequence	Taxonomic name	Comments
phylum	Annelida	worms with the body divided into segments
class	Oligochaeta	smooth worms, with short bristles
order	Terricolae	land-living worms
family	Lumbricidae	the family of earthworms and their relatives
genus	*Lumbricus*	earthworms
species	*Lumbricus terrestris*	the common earthworm

Note that the generic and the specific names should be in italics (they were not in the incorrect version), and that all of the taxonomic names, except the specific name, should begin with a capital letter.

SAQ 9 (*Objective 7*) No. The term is reserved for a cluster of different species of organisms, not for different phenotypes of the same species.

SAQ 10 (*Objective 8*) (a) Micro-evolutionary studies concentrate upon the changes that occur in a species of living organism over a few years; such evolution usually involves rather small changes of the organism's phenotype. Macro-evolutionary studies concentrate upon the changes that occur in fossils over thousands or millions of years; such evolutionary studies necessarily concentrate upon changes in anatomy, and these changes can be quite extensive.

(b) The interval between successive generations of the organisms has to be short, so that biologists can observe the changes that occur over large numbers of generations. This is what makes bacteria so useful for such studies. Moreover, the difference in fitness of the different phenotypes has to be great. In all of the examples chosen in Section 4.1 the non-resistant organisms were completely killed off by the selective agent whereas the resistant ones were not.

SAQ 11 (*Objective 9*) A's teeth (especially the canines) in shape resemble those of the cat more closely than those of any of the other specimens. Using the first kind of judgment discussed in Section 4.2, this suggests that A belonged to a carnivorous animal, that is, one that lived by catching and eating other animals. In fact, A is the skull of a fossil hyaena.

SAQ 12 (*Objective 10*) There are several acceptable answers to this question. Two of the most obvious are:

oldest ⟶ *most recent*

(i) B ⟶ F ⟶ A ⟶ E ⟶ C ⟶ D

(ii) B ⟶ F ⟶ A ⟶ E ⟶ C
B ⟶ D

(i) This model assumes that the rate and direction of evolution are variable. B evolved into F by acquiring a swelling at the end of the bone that formerly lacked one. Through A, E and C, a swelling

evolved in the middle of the bone, becoming successively larger in the three specimens. (There is nothing to stop you rotating A so that the swelling points upwards.) The swelling at the end of the bone shows no change through A, E and C. The direction of evolution then reverses, and D evolves from C by losing the swelling at one end.

(ii) This model assumes a constant direction but variable rate of evolution. The evolutionary sequence from B to C is as in (i). D however evolves along a separate line. Whereas the B–C line rapidly develops a second swelling at the end of the bone, the B–D line does not.

SAQ 13 (*Objective 11*) It was bipedal. The pelvic bones on each side have a broad, flared ilium, very like the human ilium, and the downward pointing bones are relatively short. In fact, this is the pelvis of *Australopithecus africanus*.

The answer to Exercise 2 is overleaf.

SAQ 14 (*Objective 12*) (a) E. An early hominoid, like *Ramapithecus*, has a slightly vee-shaped tooth row.

(b) C. A late hominid, like *Homo erectus* has a rounded tooth row.

SAQ 15 (*Objective 12*) A is the more closely related. Compared with B its teeth are much more uniform in appearance. A is in fact *H. erectus*, whereas B is a fossil gibbon.

SAQ 16 (*Objective 13*) The order is (brain sizes are given in brackets):

A. africanus	(450–600 cm^3)
H. erectus	(775–1 300 cm^3)
H. sapiens sapiens	(1 450 cm^3)
H. sapiens neanderthalensis	(1 300–1 700 cm^3)

Answer to Exercise 2

This tests Objective 14.

1 No. 1470 belongs to the genus *Homo* and is older than *A. africanus* (2 million years old compared with about one and three-quarter million years for *A. africanus*).

2 Yes. The flared shape of the pelvic bones is characteristic of habitually bipedal animals.

3 Because Lucy's teeth are so like those of *Ramapithecus*, she may well be directly descended from *Ramapithecus*. The similarity in their teeth is striking, particularly if you consider how much older *Ramapithecus* is than Lucy. None the less, Lucy has evolved the characteristic dentition of later hominids such as *Homo erectus*. Also at 3 million years she is quite old. Lucy was therefore probably descended from *Ramapithecus*, but more primitive than hominids such as *Homo habilis* and *Homo erectus*.

4 Yes. Lucy has skeletal features that are intermediate, between *Ramapithecus* and the earliest *Homo*, *Homo habilis*. She is also intermediate in age, coming between *Ramapithecus* and *Homo habilis*.

5 Because without an African specimen of *H. erectus* it might be argued that all of the earlier hominid finds from Ethiopia and East Africa were an evolutionary dead-end and that the final stages of human evolution took place elsewhere.

6 Your evolutionary tree should resemble Figure 31. Note how both Lucy and LH2 and LH4 belong to *Australopithecus afarensis*, which is the ancestor of both the later *Australopithecus* species and *Homo*. There is, therefore, a series of fossils, beginning with early *Australopithecus* specimens such as LH2, LH4, and Lucy, running through 1470, *Homo habilis* and *Homo erectus* to *Homo sapiens*. *Australopithecus africanus* and *A. robustus* are on a side branch, which does not lead to modern human beings.

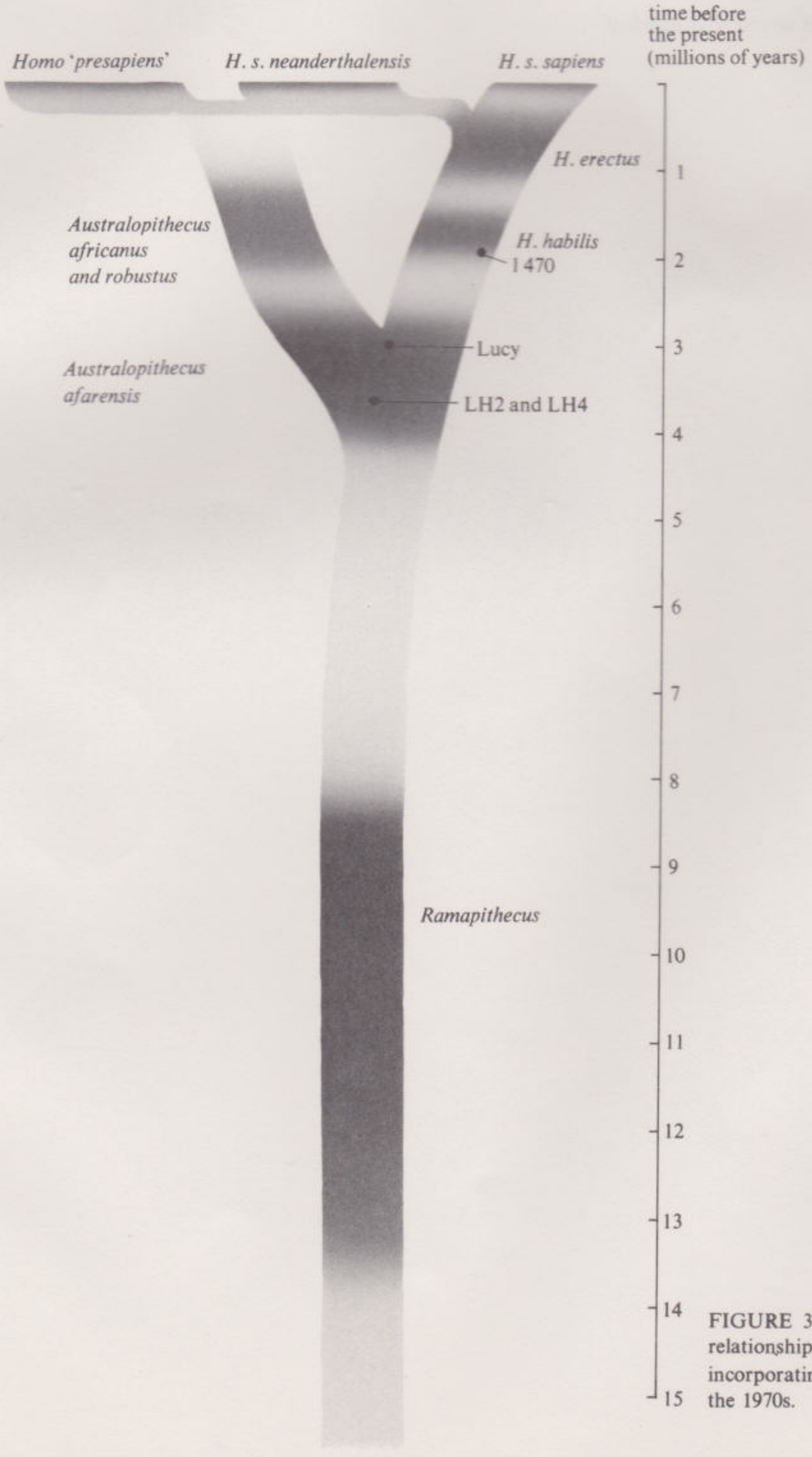


FIGURE 31 Tentative evolutionary relationships of fossil hominoids, incorporating fossils discovered during the 1970s.

Acknowledgements

Grateful acknowledgement is made to the following sources for permission to reproduce material in this Unit:

Figures

Figure 3 Society for the Study of Evolution, University of Kansas; *Figures 15, 21 and 24* by courtesy of the Natural History Museum; *Figure 16* from D. Brothwell (1976) *The Rise of Man*, Grisewood and Dempsey Ltd.; *Figure 19* from J. Buettner-Janusch (1966) *Origins of Man*, John Wiley & Sons, by courtesy of E. L. Simons; *Figure 23* from D. Pilbeam (1972) *Ascent of Man*, Macmillan, N.Y.; *Figure 25* adapted from J. E. Pfeiffer (1969) *The Emergence of Man*, copyright © 1966 J. E. Pfeiffer: reprinted by permission of Harper & Row Publishers Inc.

Filmstrips

Frames 1–4 courtesy of Dr D. T. Parkin; *Frames 8–21* courtesy of the Natural History Museum.

List of Filmstrips for Unit 20

Filmstrip 20.1,	Frame 1	*Geospiza magnirostris.*
	Frame 2	*Geospiza fortis.*
	Frame 3	*Geospiza fuliginosa.*
	Frame 4	*Certhidea olivacea.*
	Frame 5	A noctuid moth.
	Frame 6	More noctuid moths.
	Frame 7	A hawk moth.
Filmstrip 20.2,	Frame 8	*Dryopithecus* lower jaw (top); *Ramapithecus* lower jaw (centre); modern human lower jaw (bottom).
	Frame 9	*Australopithecus robustus* skull, lateral view (right), plus *A. africanus* skull, lateral view and occlusal view of mandible (left).
	Frame 10	Innominate bone of chimpanzee (left), *A. africanus* (centre) and modern human being (right).
	Frame 11	*Homo habilis* mandible.
Filmstrip 20.3,	Frame 12	Stone flake (left) and chopper (right).
	Frame 13	Peking Man. Lateral view of skull plus mandible.
	Frame 14	Peking Man. Occlusal view of palate and mandible.
	Frame 15	Skulls of Steinheim (left), la Ferrassie (centre) and Cro-Magnon Man (right), lateral views.
Filmstrip 20.4,	Frame 16	Lateral view of modern human mandible.
	Frame 17	Skull of 1470.
	Frame 18	Lower jaw of Lucy (*A. afarensis*).
	Frame 19	Occlusal view lower jaw LH2.
Filmstrip 20.5,	Frame 20	Lateral view cranium of Olduvai hominid 9.
	Frame 21	Skull of *Homo erectus.*
	Frame 22	Petralona skull.

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